DEMOGRAPHY AND ECOLOGY OF A DECLINING ENDEMIC:

THE OLYMPIC MARMOT.

By

Suzanne Cox Griffin

Bachelor of Arts, University of Montana, Missoula, MT 2001

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Approved by:

Dr. David A. Strobel, Dean
Graduate School

L. Scott Mills, Co-Chair
Department of Ecosystem and Conservation Sciences

Mark L. Taper, Co-Chair
Department of Ecology, Montana State University

Fred W. Allendorf
Division of Biological Sciences

Elizabeth Crone
Department of Ecosystem and Conservation Sciences

David Naugle
Department of Ecosystem and Conservation Sciences

Dirk H. Van Vuren
Department of Wildlife, Fish, and Conservation, UC Davis

Griffin, Suzanne C., Ph.D., December 2007   *Fish and Wildlife Biology*

Demography and ecology of a declining endemic: The Olympic marmot.

Co-Chairperson: L. Scott Mills

Co-Chairperson: Mark L. Taper

  Protected areas serve to conserve species, habitats, and ecological processes. However, biological systems within even large parks are increasingly affected by outside perturbations.

  The Olympic marmots (*Marmota olympus*) are ground-dwelling squirrel that inhabit high-elevation meadows almost exclusively within Olympic National Park Despite this protection, anecdotal reports in the 1990's of disappearances from historically occupied locations suggested that the species was in decline. I used demographic monitoring, habitat surveys, and non-invasive genetic sampling to evaluate population status of the species and consider the effects of several possible stressors.

  Olympic marmots disappeared from ~50% of well-studied colonies, and abandoned burrow complexes were common throughout the park. Estimated annual abundances at intensively studied sites indicated a currently declining population, as did population projections based on measured demographic rates. Low dispersal rates and the spatial distribution of the abandoned sites were inconsistent with metapopulation dynamics as the cause of the declines. There was no evidence that disturbance by tourists was responsible – although marmot behavior differed between remote and regularly-visited sites, there was no corresponding difference in birth or death rates. Likewise, 100% overwinter survival of adults and normal reproductive and juvenile survival rates provide no support for the hypothesis that changes in forage quality or thermal conditions within hibernacula associated with low snowpack were causing the decline. In fact, consecutive year breeding by females during years of early snowmelt suggest a possible positive effect of climate warming. Adult female annual survival was only 0.69, all mortality appeared to be due to predation with coyotes the most common predator, and even moderate changes in adult female mortality rates translated to large changes in projected population growth rates, so it is likely that coyotes are the primary driver of local Olympic marmot declines. Given that marmot populations appear depressed throughout Olympic National Park and that marmots constitute a considerable portion of coyotes diet in many parts of the park (Witczuk 2007), it is likely that this non-native, generalist carnivore is threatening the marmot's existence throughout its range.

  As parks become increasingly isolated and surrounded by human perturbations, it will be ever more important to monitor species of special interest within these areas; and when a threat is suspected, to consider more than just the most obvious candidates.

Dedication

To my husband Paul,

whose endless patience, encouragement,

and sacrifice made this possible

To my children Orion and Alpine,

with the hope that a little piece of the wild

will remain when you are grown

And to the high-country everywhere, and those that make it their home –

your beauty, strength, and endurance are my greatest inspirations

ACKNOWLEDGEMENTS

I owe much to my committee and other academic colleagues. Scott Mills and Mark Taper allowed me to pursue my dream of studying marmots – they took me on as a joint student, connected me with the park, and helped me obtain funding. They and the rest of my committee – Fred Allendorf, Elizabeth Crone, Dave Naugle and Dirk VanVuren – challenged me, encouraged me, and reined me in when necessary. Dirk provided valuable insights into marmots and, most importantly, has been a wonderful mentor. Ken Armitage and Andrew Bryant were also generous with their vast knowledge of marmots and each found time to critique my work. John Citta, Steve Hoekman, Brett Walker, and the Mills' lab provided valuable feedback and intellectual stimulus. Dan Pletcher listened when I needed an ear and encouraged me when I needed a push.

Pat Bristol, Patti Loewen, and Jodi Todd held my hand through the morass of regulations and paperwork associated with a large project with many funding sources. Their patience and competence made this possible. Similarly, Jeanne Franz guided me through the graduate school and university requirements, rescued me from many crises, and provided me with too many treats.

scientists-in-a-different-field. My son Orion assisted with field work and provided a perspective that only a small child can. Most recently, little Alpine, age 10 weeks as of this writing, slept all night, every night. And many years ago, my mother let me play in the woods and taught me to love animals – although I don't think she had giant rodents in mind!

PREFACE

A primary driver of extinctions, particularly in North America where hunting is strictly controlled, is habitat loss or degradation (Wilcove et al. 1998). Thus, parks and other protected areas serve an important role in conserving species, habitats and ecological processes. However, even the largest parks do not operate in isolation from the human dominated landscapes outside their borders. As external ecosystems become increasingly disturbed, the climate continues to change, non-indigenous species encroach upon protected areas, and recreational use of wildlands increases, parks will be faced with difficult management decisions.

When I began studying Olympic marmots (*Marmota olympus*), which are endemic to Olympic National Park, I considered them a useful species for modeling movement in the landscape and investigating the potential effects of future climate change using demographic and genetic tools. My intention was to investigate the role that landscape plays in controlling connectivity among local populations using a new framework that acknowledged the importance of within-patch dynamics in shaping dispersal patterns. To accomplish this, my specific objectives were: 1) to estimate observed marmot vital rates (birth, death, and movement rates) ; 2) to develop and test a GIS-based habitat model to identify suitable sites for marmots; 3) to determine the range-wide genetic structure of the species; 4) to develop a computer model that simulated gene flow within a metapopulation, using the demographic parameters estimated in Objective 1 and the habitat distribution determined in Objective 2; 5) to select and parameterize the model that best described how marmots move across the landscape given the observed

within population vital rates, the distribution of habitat patches across the landscape, and the observed genetic distances between populations; 6) to project marmot population structure under future climate change scenarios; and 7) to collaborate with Olympic National Park personnel to design a management plan for Olympic marmots, incorporating data on habitat, demography, connectivity, and predicted response to climate change.

This initial study plan relied on demographic rates from a stable population with which to parameterize the simulation model. I assumed the high degree of protection afforded by the nation's fourth largest national park would assure that the marmot population was currently at equilibrium. Instead I found that the Olympic marmot was missing from many long-occupied locations, that abundance was lower than previously recorded in areas where they remained, and that numbers were currently declining. Several possible causes of this decline presented themselves. Both climate change and human disturbance were potential concerns: High-elevation snowpack in the Olympic Mountains has decreased dramatically over the last 40 years (Appendix A) and it has been suggested that marmot overwinter survival depends on substantial snowpack to insulate the burrows (e.g., Barash 1989b); also, snowpack changes are expected to alter vegetation composition and productivity (Nakawatase & Peterson 2006). Recreation levels have also increased, with the marmots' high-elevation meadows a popular destination. Finally, concurrent with the arrival of large numbers of European settlers on the Olympic Peninsula, heavy logging of the lowland forests, and the extirpation of wolves (*Canis lupus*), coyotes (*Canis latrans*) arrived on the peninsula (Sheffer 1995). Coyotes eventually made their way into every corner of the park, where they are now

relatively common. Coyotes are efficient generalist predators with the potential to affect populations of new prey that they encounter as they expand their range (Gompper 2002).

With these potential identified stressors, coupled to observed present and ongoing marmot declines, the Olympic marmot system was no longer a model of how an undisturbed metapopulation functions. Instead, it became a model for diagnosing declines and managing endemic species in "protected areas" threatened by ubiquitous external forces. I thus redirected my efforts towards developing a comprehensive understanding of the spatial extent, severity, and causes of the decline. My specific objectives became: 1) to determine if the declines and extinctions observed at few sites were part of an ongoing range-wide decline, a local phenomenon, or a result of natural metapopulation dynamics; 2) to evaluate the evidence for several hypotheses about the cause of the decline; and 3) to develop a model to identify suitable habitat for the marmot to guide monitoring and recovery efforts.

In Chapter 1, I establish that the Olympic marmot has declined across its range and that these declines are ongoing. I use four different lines of evidence to evaluate the status of the species at multiple spatial scales. My overall goal was to synthesize these four measures and, in doing so, to evaluate whether the patterns I documented reflect real declines versus an alternative hypothesis that the patterns were merely manifestations of natural metapopulation processes. All lines of evidence suggested that Olympic marmots have undergone local and range-wide declines over the last 10 – 15 years. However, marmots have been postulated to exhibit classic metapopulation dynamics (Bryant & Janz 1996; Ozgul et al. 2006) and any evaluation of status that relies on occupancy rates must consider whether the observed occupancy patterns represent equilibrium

background extinction and colonization patterns. A qualitative analysis of the spatial and temporal distribution of the observed extinctions and recolonizations, dispersal patterns, and demographic rates in the context of other stable and declining populations of marmots all suggest that this is not the case. Alone, no one of the four lines of evidence that I present would absolutely demonstrate that Olympic marmots are in a sustained decline across their range. However, each is consistent with such a decline, while the spatial pattern of the extinctions is inconsistent with metapopulation dynamics of a population at equilibrium. In effect, by considering multiple metrics of distribution and demography, as well as how the observed patterns compare to those seen in other species of marmots, I have reduced the uncertainty about Olympic marmot population status to a negligible level. Roger Hoffman (Olympic National Park GIS specialist) contributed his GIS skills to the project, generating the maps used to guide the range-wide surveys and is a co-author, along with Mark Taper and Scott Mills on the resulting manuscript.

In chapters 2, 3, and 4, I evaluate the evidence for several potential causes of the declines. In chapter 2, I investigate the effects of high levels of tourism on Olympic marmots. High levels of recreation are thought to negatively impact many species (e.g., Klein et al. 1996; Müllner et al. 2004) and were found to be associated with changes in Olympic marmot behavior. However, if changes in animal behavior resulting from direct human disturbance are to negatively affect the persistence of a population, these changes must lead to reduced demographic performance (Gill et al. 2001). In the case of Olympic marmots, demographic data showed that behavioral changes were not associated with decreased survival, reproduction, or body condition. Our results demonstrate the importance of evaluating both behavioral and demographic data when evaluating the

effects of tourism on wildlife species. Tanguy Valois, an international student intern (from France), contributed to the design of the behavioral study and made most of the associated observations. He is co-author, along with S. Mills and M. Taper, on the resulting publication in *Conservation Biology* (Griffin et al. 2007b).

In chapter 3 I report on several observations of consecutive year reproduction by Olympic marmot females, casting doubt on the hypothesis that the observed decline is directly caused by decreased snowpack under climate change. Olympic marmots had previously been reported to skip at least one year between reproductive efforts (Barash 1973, 1989b), but I observed several female marmots weaning infants in consecutive years. All second litters were observed in years of unusually low spring snowpack. Although these observations do not preclude the possibility that climate change will negatively influence marmot demographic rates, they suggest that increased spring food availability resulting from climate change may actually allow females to wean consecutive litters regularly. S. Mills and M. Taper are co-authors on the resulting publication in *American Midland Naturalist* (Griffin et al. 2007a).

In chapter 4, I argue that heavy predation by a non-native predator, the coyote, has caused populations of the relatively naïve Olympic marmot to decline. Data from radio-tagged marmots indicate that coyotes are the most common predators on marmots. Experimental manipulations of a demographic matrix projection model further suggest that even modest predator mortality is likely to cause marmot population growth rates to decline substantially. These findings are supported by Witczuk (2007) who performed genetic and diet analyses on carnivore scats across the park and found that coyote scat was the most common carnivore scat in the high country, that coyote scat regularly

contained marmots, and that almost all coyotes included marmots in their diets. Collectively, these results are consistent with the hypothesis that the current level of coyote predation is a significant stressor on intensively monitored Olympic marmot populations. These results will be incorporated into a manuscript along with the results from Witzcuk (2007).

For any declining species, future persistence depends on reversing the deterministic drivers of decline and on monitoring to evaluate the progress of recovery. The first fundamental step in any such monitoring program includes determining potential habitat to be sampled. Therefore, as the last chapter (Chapter 5) of my dissertation documenting the decline of a national park endemic, I describe a novel approach to building a habitat suitability model. The Mahalanobis distance statistic has been successfully applied to identify suitable habitat when only presence data were available (e.g., Clark et al. 1993; Tsoar et al. 2007; van Manen et al. 2005) but its usefulness has been hampered by the lack of a method for identifying the best subset of explanatory variables. We developed an approach to identify the best combination of these variables, and present a metric that allowed us to quantitatively compare the specificity of multiple Mahalanobis distance models. We successfully applied this approach to Olympic marmot habitat. R. Hoffman contributed substantially to this effort, writing the ALM code to compute Mahalanobis distance scores for the entire study area and participating in early discussions about how to use the available data to model Olympic marmot habitat.

In this dissertation, I present the analyses of a considerable amount of demographic and distribution data. These analyses, in conjunction with Witczuk's (2007)

thesis, should provide park managers with the information needed to understand the scope of the decline and to allow them to address the proximate cause of the decline. As part of the original study objectives, I also collected tissue and hair samples for genetic analysis from several hundred additional marmots representing the majority of the known Olympic marmot colonies. Laboratory analyses of these samples are ongoing and not presented in this dissertation, although basin information on number of samples collected, loci screened, amplification conditions, and allelic diversity are presented in Appendix G. Future analyses of these samples should add important information on population structure, inbreeding effects, and population trends at remote sites and should be undertaken as soon as feasible.

As human activity alters ecological processes at increasingly large scales, even the largest protected areas are being threatened by external perturbations. Yet it is not always obvious when external forces will impact protected areas, nor which will have the greatest impact on a given species. I incorrectly assumed that Olympic marmots were relatively isolated from external forces, as >90% of the species range is protected. Once the decline was suspected and then confirmed (Chapter 1), tourist disturbance or climate change was initially suspected to be driving the decline. Contrary to predicted influences of climate warming, I did not find that low snowpacks reduced birth rates (Chapter 3) or overwinter survival (Chapter 1). Similarly, tourism did not appear to be driving the decline; I found birth and death rates to be similar at heavily visited and remote sites (Chapter 2). It was only through intensive demographic study and widespread habitat survey (Chapter 1) that the extent and severity of the decline were recognized, and that predation by a non-native predator (Chapter 4) was identified as the proximate cause of

the decline. Finally, many parks have limited resources to conduct extensive presence /

absence surveys. My improvement to a habitat modeling approach that depends only on

presence data offers potential benefits in many settings, and the resulting map of suitable

habitat for Olympic marmots will facilitate future efforts to reverse the declines and

monitor the recovery of the species (Chapter 5). As our parks become increasingly

isolated in a rising sea of human perturbations, it will be ever more important to monitor

species of special interest within these areas; and when a threat is suspected, to consider

more than just the most obvious candidates.

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CHAPTER 1.

THE CASE OF THE MISSING MARMOTS: ARE METAPOPULATION DYNAMICS OR RANGE-WIDE DECLINES RESPONSIBLE?

Abstract. In the mid-1990's, anecdotal reports of Olympic marmot (*Marmota olympus*) disappearances from historically occupied locations suggested that the species might be in decline. Concern was heightened by the precipitous decline of the Vancouver Island marmot (*M. vancouverensis*), coupled with reports that climate change was affecting other high-elevation species. However, it was unclear whether the Olympic marmot was declining or undergoing natural extinctions and recolonizations; distinguishing between normal metapopulation processes and population declines in naturally fragmented species can be difficult. From 2002-2006, we used multiple approaches to evaluate the population status of the Olympic marmot. We surveyed sites for which there were records indicating regular occupancy in the later half of the 20th century and we conducted range-wide surveys of open high-elevation habitat to establish current and recent distribution. We used these targeted and general habitat surveys to identify locations and regions that have undergone extinctions or colonizations in the past 1-4 decades. Simultaneously, we conducted detailed demographic studies, using marked and radio-tagged marmots, to estimate the observed and projected current population growth rate at 9 locations. The habitat surveys indicate that local extinctions have been wide-spread and, in some places, severe. Abundance at most intensive study sites declined from 2002-2007 and the demographic data indicate that these local declines are ongoing. Adult female survival in particular is considerably lower than it was historically.

The spatial pattern of the extinctions is inconsistent with observed metapopulation dynamics in other marmot species and, together with very low observed dispersal rates, indicates that population is not at equilibrium.

INTRODUCTION

The Olympic marmot (*Marmota olympus*) is a large ground-dwelling squirrel endemic to the Olympic Peninsula, in northwest Washington State, USA. Most Olympic marmot habitat (>90%) is protected within Olympic National Park. In the mid-1990's park staff observed that the Olympic marmot had disappeared from several well-known colonies, such as those in the meadows surrounding the popular Hurricane Ridge Visitors' Center. These observations, combined with anecdotal reports from visitors that marmots were absent from some less prominent locations and the dramatic, highly publicized declines of the Vancouver Island marmot (*M. vancouverensis*; Bryant and Janz 1996), raised concern about the Olympic marmot. Reports that climate change has affected other high-elevation species, including the yellow-bellied marmot (*M. flaviventris*) (Inouye et al. 2000), added to the concern. However, Olympic marmot habitat is naturally fragmented and it remained possible that the extinctions were part of natural metapopulation process. In 1999, park biologists identified investigation of the Olympic marmot population as priority project in their Resource Management Plan.

Logical first steps in any conservation effort are to determine if the species in question is actually declining, and if so, throughout what portion of its range. Due to data limitations, many species status evaluations are based on either apparent changes in occupancy patterns, or analyses of local population trends or demography. While considerable insight can be gained from these approaches, single metrics of status can be open to the criticism that the apparent declines are idiosyncratic to the particular study sites or that normal population processes, such as extinction and colonization within a metapopulation (Hanski 1998), are responsible for perceived declines. Alternatively, declines might be missed or their detection delayed if the monitored metric is not sensitive to overall population performance (Taper et al. in press). For example, occupancy rates may remain stable for several generations after a population decrease (Conrad et al. 2001). By evaluating multiple lines of evidence, it may be possible to arrive at a robust conclusion about a population's status when no one metric is irrefutable.

In this paper, we use several types of data collected at multiple spatial scales to evaluate the status of the Olympic marmot. Beginning in 2002, we collected these distribution and detailed demographic data as part of an unrelated study. We now use these data to allow us to consider four different lines of evidence for recent range-wide declines and for ongoing declines at a smaller number of sites. Specifically: we 1) resurveyed sites for which there was reliable evidence of long-term occupancy (> 40 years) to determine if they were still occupied; 2) we surveyed habitat throughout the marmots' range to determine both recent and current distribution; 3) we examined 4-5 year abundance trends in three geographically discrete site groups; and 4) we used

survival and reproductive data and female-based matrix models to determine if

demographic rates are consistent with an ongoing decline at these sites. Our overall goal

was to synthesize these four measures and, in doing so, to evaluate qualitatively the

alternative hypotheses that the patterns we documented reflect real declines or that the

patterns were manifestations of natural metapopulation processes. Where possible, we

placed our results in the context of demographic and occupancy patterns in other marmot

species.

STUDY AREA & STUDY SPECIES

Olympic marmots are restricted to the upper slopes (>1400 m) of the Olympic

Mountains, on the Olympic Peninsula in northwest Washington State (Fig. 1). Small

groups of 3-20 marmots dig extensive burrow systems in alpine and subalpine meadows.

These meadows range in size from < 5 ha to > 100 ha and are embedded in a matrix of

forest, rock and snow. Like the closely-related hoary (*M. caligata*) and Vancouver Island

marmots, Olympic marmots hibernate for 6-8 months a year, delay any dispersal until

after the second hibernation, and only attain reproductive maturity at age three or four

(Barash 1973, 1974; Bryant 1998, 2005; Bryant & McAdie 2003). All three species

typically breed biennially, but can occasionally breed annually (Bryant 2005; Griffin et

al. 2007a; Kyle et al. 2007). In any case all show unusually low reproductive rates for a

rodent.

Much of the Olympic Peninsula, including most of the higher elevations, is

protected within Olympic National Park. Our study was restricted to park lands. There is

a steep precipitation gradient from southwest to northeast across the peninsula: annual

precipitation averages 600 cm of precipitation on Mt. Olympus while as little as 50 cm

falls on the northeast corner. Eighty percent of this precipitation falls between October

and March, mostly as snow above 750 m (Houston & Schreiner 1994b). Even in the

relatively dry northeast, snowpack lingers well into summer in the high-country. Several

large rivers drain the central Olympic Mountains and have carved deep, steep-sided

valleys that appear to act as barriers to marmot movement (S. C. Griffin et al.,

unpublished genetic data). The peninsula is surrounded by water on three sides and

extensive lowland forest on the fourth – as a result, there are numerous endemic plant and

animal species and subspecies on the peninsula, and the mammalian fauna in particular is

impoverished relative to the mainland (Houston et al. 1994a).

METHODS

Surveys of historically recorded colonies

As a first step in assessing Olympic marmot population status, we resurveyed

historically recorded colonies. These sites were all in readily accessible areas of the

northeast region of the park and have been periodically studied since the 1950's.

Although marmot presence had been recorded in ≥ 1 year at 31 colonies, we restricted

our inference to the 25 sites that we were able to relocate confidently and where presence

had been recorded ≥ 2 times between 1950 and 1996 ($\bar{x} = 3.84$, sd = 1.86; Table 1). We

were assisted in relocating colonies by J. Burger, who had conducted a presence absence

survey in 1989 (Houston & Schreiner 1994a) and at that time had received guidance from

two previous researchers (W. Wood and D. Barash).

In early 2002, we visited each of the 25 sites. Field workers typically watched sites for about 30 minutes from a good vantage point prior to 1100 hours or after 1600 hours, and then traversed the area on foot looking for active or abandoned burrows. Our extensive experience at occupied sites indicated that marmots are rarely below ground for >30 minutes during these hours. Burrows are always visible, often from > 100 m, and regularly used burrows often have signs of occupancy, including evidence of recent excavation (fresh dirt and rocks in the entrance) or marmot scat in or near the mouth of the burrow. At occupied sites in the Hurricane Hill and Obstruction Point areas, we then initiated demographic studies (see below), negating the need for further presence-absence surveys. Sites where we did not find marmots were visited ≥ 1 additional time in 2002, with additional visits in subsequent years through 2006. Many sites were also visible from roads that we regularly traveled (Table 1) – these sites were scanned for marmots at least weekly. Park ranger, education, and campground staff also visited most abandoned colonies weekly or even daily in the course of their usual activities and reported to us any unusual activity, marmot or otherwise. Given the high visibility of marmots and their burrows, and the regular observation of these sites, we consider it almost impossible that marmots were present and not detected.

Range-wide habitat surveys

To determine the current and recent distribution of Olympic marmots, we systematically surveyed potential marmot habitat throughout the park. At the start of the study we had limited knowledge of the requirements of Olympic marmots, so we used very broad criteria to select potential habitat. Based on details from Barash (1973) and

Wood (1973), and personal observations from 2001 (SCG) we assumed that marmots use

high-elevation meadows with or without rock. Specifically we designated as potential

habitat all areas of meadow, bare ground, or rock 1400 -2157 m elevation. The upper

elevation limit represents the upper limit of meadow, and thus food for the marmots, in

the Olympic Mountains. We subdivided the resulting habitat patches by aspect – patches

were split at 45°, 135°, 225°, and 315° – and eliminated any patch < 9 pixels (0.56 ha;

approximately the minimum Olympic marmot home range) (Griffin 2007). We used

1:24,000 topographic maps to subjectively classified the resulting 3516 polygons as

inaccessible (n = 1845), difficult to access (n = 880), and readily accessible (n = 791)

based on distance to a trail, the steepness of the polygon, and the apparent ruggedness of

the surrounding terrain. Polygons deemed inaccessible were removed from the selection

process.

We stratified these remaining polygons according to slope (two classes: < 30%, $\geq$

30%), aspect (four classes described above), area (3 classes: < 25,000 m^2, 25,000 –

90,000 m^2, > 90,000 m^2) and region (four classes: Fig. 1). We used random numbers to

select "primary" polygons for survey from each of these 96 slope-aspect-area-region

combinations (hereafter, stratification cells); six readily accessible polygons were chosen

for each difficult to access polygon. We selected four primary polygons per stratification

cell in the NW and NE, three per cell in the SW, and two per cell in the SE, a ratio

roughly proportional to the total number of polygons in each region. A few stratification

cells contained fewer than the desired number of primary polygons, with the result that

302 primary polygons were selected for survey. Our assessment of access difficulty was

not perfect; when a primary plot proved inaccessible in the field, we substituted another by moving down the list of ordered random numbers.

In addition to the primary polygons, we also surveyed up to four "secondary" plots in the vicinity of each primary plot. In many cases, there were fewer than four secondary polygons available within a reasonable radius ("reasonable" was terrain dependent but generally <1 km), or the density of primary polygons in an area was such that there were insufficient numbers of secondary polygons available. We also surveyed areas inside and outside the polygons where marmots or burrows had been reported in the past and additional polygons (including 46 classified as inaccessible) on an opportunistic basis. A few of these (collectively, "opportunistic") surveys took place in 2001 and 2006.

Selected polygons were visited on foot to determine occupancy status (occupied, abandoned, no sign). Field crew used maps and satellite images to visually identify he boundaries of the selected polygons and then walked rough transects across the polygon at approximately 20 m spacing, searching for marmots or burrows. Marmot burrows are often located beneath large rocks or are surrounded by large, diagnostic dirt mounds, which can be > 1 meter high and > 3 m across (S. C. Griffin et al., *unpublished data*, Fig. 2). These mounds typically have a compacted, bare porch surrounded by dark green sedge (*Carex spectabilis*), making them visible from a considerable distance. The mountain beaver (*Aplodontia rufa*), which is abundant in the Olympic Mountains and makes slightly smaller diameter burrows, occupies wetter habitats than marmots do, leaves the excavated dirt in pyramid shaped piles, and typically digs numerous entrances in various stages of collapse which honeycomb small sections of hillside. It is difficult for a person with even minimal experience to confuse the two types of burrows.

Current occupation of marmot burrows was confirmed by the presence of: scat in the entrance; recent digging activity; characteristic flies or strong marmot odor in the entrance; marmot tracks, compacted and clipped grass on the mound; or trails of compressed vegetation between burrows. Abandoned marmot burrows could often be similarly diagnosed, although eventually the vegetation reverts to forbs, heather, or grass and the burrow entrances collapse. The rate of these changes appears to vary according to site conditions so precise dating of the last use is not possible; most abandoned burrows are probably undetectable after 7-15 years.

When marmots were found, locations of representative marmots or burrows were usually taken with a handheld GPS unit (generally accurate to ±10 m) and the search of that polygon was terminated. We conducted a X^2 test for overall differences in the proportions of occupied, abandoned, and no sign polygons among the four regions. We followed this with pairwise tests for differences in the proportions of polygons that showed some sign of marmot activity (occupied and abandoned pooled) and those that showed no sign of marmot activity between each pair of regions, and pairwise tests for differences in the proportion of occupied and abandoned polygons between each pair of regions. We Bonferroni adjusted our alpha-level to $P = 0.004$ to control for Type 1 errors among these 12 pairwise tests (Sokal & Rohlf 1995).

While we assumed that if marmots or active burrows were found, a polygon was unequivocally occupied, it is possible that we failed to detect marmots or abandoned burrows in some occupied or abandoned polygons. These errors, if common, could lead to an underestimate of currently occupied habitat and an overestimate of the severity of a decline (MacKenzie et al. 2006). Although Witczuk (2007) estimated a >90% detection

rate for Olympic marmots, we independently investigated the potential effect of misclassification of occupied polygons in our data set. We had two independent observers visit 55 polygons in the same year, and then used adjusted Lincoln-Peterson models (Chapman 1951) to estimate the single visit detection probability for an occupied polygon and the single visit detection probability for an abandoned polygon. We used these detection probabilities to explore how much we may have underestimated the proportion of occupied and abandoned polygons.

Demographic study sites

We used data from intensively-studied, marked animals at 3 geographically distinct groups of sites to estimate birth, death, and movement rates and population trends over 4-5 years. The Western site group consisted of 1) Hurricane Hill, where there was a cluster of several adjacent, often interacting colonies (elevation ~1600-1750m; all aspects), 2) a single colony "Picnic" at the Wolf Creek picnic area (~1520 m, south-facing), and 3) a single colony in Sunrise Basin (~1600 m, east-facing). Earlier studies (Barash 1973; Griffin et al. 2007b), including the historic colony inventories (Table 1), have considered individual family groups on Hurricane Hill and in Sunrise Basin; our demographic analyses would not have differed as a result of this subdivision and the fluidity of some family groups would have complicated study site definition, so we considered each of these contiguous areas as a single site. Hurricane Hill, Picnic, and Sunrise Basin were all within 3.3 km of each other in the vicinity of the Hurricane Ridge Visitors Center and all were studied beginning in spring 2002. With the exception of one or two marmots in a basin adjacent to Hurricane Hill, there are no other known marmot

colonies < 3.5 km of this group. Demographic data were available from earlier studies of these colonies (Barash 1973; Wood 1973).

The Central group was >10 km south-east of the Western group and consisted of five sites located along or near the Obstruction Point Road. These were 1) Eagle Point (~1760 m, southwest-facing), 2) Pull-out (~1760 m, east-facing), 3) Marmot Flats (1750 m, northeast- to northwest-facing, relatively flat), 4) Obstruction Point (1830-1900 m, south- to west-facing), and 5) Pumpkin Seed Lake (1750-1820 m, west-facing basin). Eagle Point and Pull-out were occupied by single family groups, Pumpkin Seed Lake by 1-2 family groups depending on the year, and Obstruction Point and Marmot Flats were both occupied by several family groups in most years. The maximum straight-line distance between any two Central sites was 3.9 km, and no site was < 1200 m from another. Studies began at these sites in late-spring 2002, with the exception of Pumpkin Seed Lake and Pull-out, which we first studied in summer 2003. There are other marmot colonies in the area, although we never detected any immigrants into our study colonies. These sites were chosen for study primarily out of convenience – they were the only currently occupied colonies near a road (although the road is closed until July due to snow).

The final study area was in Royal Basin, >15 km to the southeast of the nearest Central group site and 13 km from the nearest (remote) trailhead. Marmots were found throughout this large basin but our study area was a steep, east-facing meadow (1630-1770 m) where marmot densities were particularly high. We began work here in 2003 after it became obvious that the Western and Central sites did not encompass the full range of Olympic marmot densities and habitat types.

Trapping, marking, and implantation of radio-transmitters

We attempted to eartag all marmots at the demographic sites, and we implanted a subset with radio-transmitters. We generally followed trapping and handling procedures outlined in Bryant (1996), with exceptions described in Griffin et al. (2007b). We classified marmots as juvenile, 1 year-old, 2 year-old, or adult, indicating that they had completed 0, 1, 2, or $\geq$ 3 hibernations respectively. We collectively refer to 1 and 2 year-olds as subadults – these age classes do not depend on parental care but are not yet reproductively active. Field aging at first capture for non-juveniles was verified with an algorithm developed from morphometric data collected on known aged animals (Griffin 2007).

We surgically implanted 40-g radio transmitters in the peritoneal cavity of 102 marmots $\geq$ 1 year-old, following published surgical methods (Bryant & Page 2005; Van Vuren 1989). These transmitters have not been found to influence marmot survival or reproduction (Bryant & Page 2005, S. C. Griffin et al., unpublished data; Van Vuren 1989). The signal from transmitter of one marmot was never detected following surgery; we removed this animal from the data set, leaving 101 marmots. Eighteen marmots received second surgeries to replace aging or failed transmitters.

Survival and reproduction

We confirmed the status (alive or dead) of marmots with radio implants at least twice per month during the active season, except during September 2002 and May 2003, when status was checked only once per month. We found three transmitters beneath the

snow outside burrows in May 2003 – these animals were presumed to have died prior to initiating hibernation in September 2002.

We used known-fate models in the program Mark (White & Burnham 1999) to estimate survival in ten 0.5-month active season intervals (1 May – 1 October) and the winter period. From these, we obtained annual survival rates for adult males, adult females, and subadults. We considered patterns observed in marmots and other species in formulating the candidate model set (Appendix C). Various models included possible effects on survival of spatial autocorrelation in environmental conditions or predator abundance among site groups, effects of age and sex class (adult females, adult males, and subadults), and seasonal differences for one or more age / sex classes (Bryant & Page 2005; Griffin et al. 2007b; Hoogland et al. 2006). Because a model that included separate parameters for September survival of all marmots and June survival of adult females had previously performed well on a subset of this data (Griffin et al. 2007b), we included three models with these parameters in our candidate model set. No radio-implanted marmot died during hibernation, so a single parameter for over-winter survival was applied to all sites and age/sex classes in every model.

We used two measures of reproductive success: weaning success (the proportion of females present in late-June that weaned litters) and litter size (for details see, Griffin et al. 2007a). In cases where logistics prevented checking females at <10 day intervals, if the mobility of infants when we discovered them suggested that they had been above ground for ≥ 10 days, we excluded the litters ($n = 8$) from the analysis of litter size as some infants might have already been lost to predation. We assumed that the sex-ratio of marmots captured as juveniles was representative of the population at birth. We only used

data from animals that were sedated when sexed as juveniles, as sex determination on unsedated juveniles proved to be unreliable.

We determined apparent survival for each juvenile from initial tagging in the year of its birth until the following spring, based on whether the animal was trapped or resighted, either opportunistically or in a resighting session (see *Estimating abundance* below) in May or June. No tagged yearling that we failed to detect prior to 1 July was later trapped or resighted. Because some juveniles may have died prior to tagging, we also estimated survival based on the number of juveniles appearing above ground and the number seen the following spring, omitting litters for which we were not confident that we had fully counted the litter.

Reproductive rates and juvenile survival rates were determined for each site group and for the entire population. We used X^2 or one-way analysis of variance (ANOVA), as appropriate, to test for differences among site groups.

Estimating abundance

We used two approaches to estimate abundance of non-juveniles for each site / season / year combination. First, we used data from mark-recapture type "resighting" sessions in robust design models (Pollock 1982) to estimate abundance ($\hat{N}$). Following initial marking of the population, resightings were conducted in June and August of all years at all sites except Royal Basin, where dangerous snow conditions prohibited extensive work in June 2006. Each "encounter session" was 2-4 hour-long. In each encounter session 1-3 people attempted to positively identify all marmots present by reading their eartags with binoculars or a spotting scope. Three encounter sessions were

conducted at each site per secondary session. Second, we combined records from all

sources (trapping, telemetry, opportunistic sightings, and resightings) to arrive at a

minimum number alive (MNA) for each site in spring (prior to July 1) and fall (August 1

to initiation of hibernation) of each year. These 2-month periods cannot be considered

closed (i.e., deaths could occur) so if detection rates were high, MNA could exceed $\hat{N}$

without indicating that $\hat{N}$ was biased.

We analyzed the closed population portion of the resighting data with Huggins

full heterogeneity models in program Mark (White & Burnham 1999). The Huggins

models allow detection probability to vary among and within secondary sessions; initial

capture probabilities to differ from recapture probabilities; and a mixture of two groups

with different capture probabilities. The open population parameters in these models

estimate survival and migration. Estimated abundance $\hat{N}_i$ within each secondary session

i, is a derived parameter.

For these analyses, we subdivided the Central and Western site groups as follows:

Central-A included the three Central sites where we began studies in 2002 (Eagle Point,

Marmot Flats, and Obstruction Point), and Central-B included the two sites where we

began work in 2003 (Pull-out and Pumpkin Seed Lake). Because Picnic and Sunrise

Basin were extinct or functionally extinct for much of the study, we only conducted

regular resightings at Hurricane Hill. Therefore, MNA is presented separately for each

Western site and $\hat{N}$ is only presented for Hurricane Hill. We fit a slightly different suite

of candidate models for each site group to account for differences in data structure and

quantity (Appendix D). For all models with $\Delta AIC_c \leq 2$, we examined the model

structure, estimates of $\hat{N}$, and associated 95% confidence intervals for each site group to

identify the model from which we ultimately derived estimates of $\hat{N}$. When these highly-ranked models differed by only a single parameter, we followed the recommendation of Burnham and Anderson (2002) and relied on estimates from the least parameterized of the models.

Estimation of population growth rates

We used a diffusion analysis approach (Dennis et al. 1991; Morris & Doak 2002) to determine the average estimated intrinsic growth rate ($\hat{\bar{r}}$) and associated standard errors for each site group (or subgroup) separately based on each of spring MNA, fall MNA, spring $\hat{N}$, and fall $\hat{N}$. For the spring MNA estimates, we included a projected MNA for spring 2007. This number is MNA fall 2006 plus 2006 juveniles seen in September, minus any animals known to have died during the fall (Taper & Gogan 2002). If marmots without radio-transmitters died, the MNA spring 2007 would be inflated. While it was possible that immigrants could increase local populations in spring 2007, this did not occur in previous years.

We also used deterministic matrix models (Morris & Doak 2002) to project population growth rate for each site group based on that group's observed demographic rates. The Central sites were modeled together. We used a pre-birth pulse census, female-based model, where the "birth pulse" is the emergence of juveniles from burrows beginning about July and the census occurs immediately post-hibernation (May). As at that time there are no juveniles present in the population, we modeled spring to spring survival of three age-classes (1 year-old, 2 year-old, adult). Adult females present at the start of year *t* produced female 1 year-olds in year *t+1* at the following rate per adult

female: *(survival adult females May 1- July 15) x (proportion of females reproducing) x (litter size) x (proportion of female pups) x (survival of juveniles from emergence to spring).* We parameterized the model for each site based on the estimated survival and reproductive rates at each site group, regardless of whether these rates differed significantly among site group. We transformed the annual asymptotic discrete population growth rate λ to the continuous time growth rate ($ln\ \lambda = r$). Age distribution on average at each site was close to the stable age distribution assumed by the asymptotic λ.

RESULTS

Historically occupied sites

Of the 25 colonies where marmots had previously been recorded in multiple years, 12 were not occupied in 2002. All occupied colonies were confirmed to be occupied at the initial visit. Three additional colonies went extinct during the course of our study: marmots disappeared from two sites in Sunrise Basin between fall 2002 and spring 2003, and the last marmot disappeared from "Picnic" in mid-summer 2006, although the absence of any male at that isolated site meant that the colony had been functionally extinct since 2002. Thus, in fall 2006, 60% (15/25) of the historically known colonies were not occupied. A 1989 survey had visited 22 of these 25 sites and found marmots at all of them (Houston & Schreiner 1994a) – thus, the extinctions we observed are a recent phenomenon. Colonies tended to go extinct in clusters; disappearances from Blue Mountain and from the areas around the Hurricane Ridge Visitor's Center accounted for 12 of the 15 extinctions. No recolonizations have been detected and no new

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areas have been known to be colonized as of fall 2006. The high visibility of many of the extinct sites and the intense interest shown by park staff, combined with the foot surveys, makes it extremely unlikely that marmots would not have been detected if they were present at, or recolonized, these sites during the course of the 5-year study.

Habitat surveys

We surveyed 282 primary, 379 secondary, and 148 opportunistic polygons. This represents 94% of all primary and 23% of the total predicted polygons. Of these 809 polygons, 244 (30%) were surveyed formally or opportunistically in multiple years ($\bar{x}$ = 1.45 years, sd = 0.88). We ultimately classified 219 polygons (27%) as occupied, 111 (14%) as abandoned, and 484 (60%) as without sign of marmots. The proportions were very similar when based on the 282 primary polygons: 30% were classified as occupied, 16% as abandoned, and 55% as without sign of marmots. In both cases the ratio of abandoned to occupied polygons was slightly greater than 0.5:1.

There were large regional differences in both the proportion of polygons that showed some sign of marmots (i.e., occupied or abandoned vs. without sign) and the ratio of abandoned to occupied habitat ($X_6^2 = 179.89, P < 0.001$; Fig. 3). The proportion of polygons in the southwest with any sign of marmots was only 11%, compared to $> 42\%$ in each of the other three regions (pairwise X^2 tests, all P's < 0.001). Of the polygons with sign of marmots, a higher proportion appeared to be abandoned in the southwest and southeast regions (76% and 58% respectively) than in the northwest and northeast regions (24% and 26% respectively; all pairwise X^2 tests, all P's < 0.001).

Fifty-five polygons were visited twice in the same year by observers who had no prior knowledge of occupancy status. Sixteen of these were classified as occupied in the first visit, 17 in the second, with 15 classified as occupied in both visits. Based on the adjusted Lincoln-Peterson estimator (Chapman 1951), the true number of these test sites that were occupied was approximately 18.1 (SE 0.38) and the single visit detection probability was 0.92, very similar to an independent estimate in the same system of a 93% detection rate (Witczuk 2007). Given a detection probability of 92%, we would expect to detect marmots in 99% of the occupied polygons visited at least twice and 92% of the occupied polygons visited once. We detected marmots at 118 single visit polygons and 101 multiple visit polygons; adjusting for detectability would lead to a minor adjustment resulting in an estimated 229 occupied polygons (i.e., 118/0.92 + 101) compared to the observed 219. This represents just a 5% increase over the unadjusted numbers – not a biologically important difference.

A similar analysis of polygons classified as abandoned in one or both of two within year surveys points to a lower single survey detection probability (0.63) for abandoned polygons but signs of prior occupancy still would be detected at >85% of abandoned polygons surveyed twice and at 95% of those polygons surveyed ≥3 times. Adjusting for this detection rate produces a corrected estimate of 159 abandoned sites, an increase of 43% from the uncorrected count of 111. The adjusted proportions of occupied, abandoned, and no sign polygons would be 28%, 20%, and 52%, increasing the ratio of abandoned to occupied to 0.7:1. While the adjusted number provides a useful upper bracket for the true number of abandoned polygons, it probably represents an overestimate, because in many cases, surveyors had prior knowledge about historic

occupancy and so may have been predisposed to recognize old burrows, possibly

increasing detection rates of abandoned burrows on sites that actually were abandoned;

by contrast, the double surveys were intentionally conducted by observers with no

knowledge of occupancy status.

Survival and reproduction

We monitored 101 subadult and adult marmots for a total of 1504 0.5-month

active season intervals (Table 2) and 124 7-month over-winter intervals. Thirty-three

marmots died during this period, the signal from 11 marmots disappeared along with the

animal, and four marmots outlived their transmitters and were subsequently recaptured.

No radio-implanted marmot died during hibernation.

Multiple lines of evidence suggested that the 11 missing animals were in fact

dead. If the transmitters had failed and the animals remained alive, our high detection

probability (see *Abundance trends*) means that we should have relocated most animals.

The 11 missing marmots were not particularly cryptic – they were trapped an average of

1.5 times each and seen in 61% of possible resighting sessions in the year prior to their

disappearance. Of the four transmitters known to have failed, three had exceeded their

expected battery life, while of the 11 missing transmitters, only two were at or near the

end of their expected battery life. The median age of the missing transmitters was less

than half their expected lifespan. Alternatively, if animals had dispersed off the study

area we would expect the 'missing' marmots to be disproportionately subadults and

males. In fact, eight of the 11 missing animals were adult females; seven of these had

weaned young in that year or previous year. We were not able to locate any missing

animals from fixed-wing aerial telemetry flights. Finally, we have recovered numerous

badly damaged although still operable transmitters from predated marmots, suggesting

that predators may bite and destroy transmitters. Given all this evidence, we treated

missing marmots as having died in the interval in which they were first missing. If

missing marmots did disperse from the study area, our survival rates would actually

represent apparent survival, a distinction that is irrelevant to the local populations given

the complete lack of immigration.

According to estimated rates derived from the top-ranked model based on the

radio-telemetry data (Appendix C), annual survival of adult females was considerably

lower than that of adult males and subadults, and survival of all animals was lower at the

Western and Central site groups than at Royal Basin (Table 2).

This model likely overestimated apparent survival rates in subadults at Royal

Basin. Our sample of implanted subadults at that remote site was limited to four 2-year-

olds implanted in June 2004 and 6 yearlings implanted in August 2006 (total 36 active

season intervals). Although none of these died or dispersed prior to age three, only 11 of

21 subadults tagged in 2003 and 2004 at Royal were subsequently detected as adults.

Many or all of the other 10 tagged marmots presumably died or dispersed.

Among the reproductive rates, only the proportion of females present in mid-July

that successfully weaned litters differed significantly among site groups

($X_2^2 = 6.13; p < 0.05$; Table 2), with the best performance at the Central sites and very

low reproduction at Royal Basin. Litter size averaged 3.31 ($n = 19$ litters), with little

variation among site groups. The sex ratio of the pups was somewhat skewed (0.58

female, $n = 59$), particularly at the Central sites where several litters were entirely female,

but did not differ significantly from 1:1. Juvenile survival from emergence through hibernation appeared similar across sites as well (0.60, $n = 89$).

Abundance trends

All site groups, with the exception of Central-B, experienced declines from the first to last season of the study, as measured by both the mark-recapture estimates of $\hat{N}$ and MNA (Fig. 4 and 5). The increase at Central-B was driven by Pumpkin Seed Lake; the other colony in the group, Pull-out, declined from four to three marmots from fall 2003 – fall 2006. Two sites in the Western site groups, Sunrise and Picnic, became extinct during the study.

The structure of the mark-resight models used to estimate abundance differed across site groups (Appendix D), reflecting differences in the candidate models sets, resighting conditions, and variation in sample sizes at the different site groups. As expected, daily detection probabilities varied considerably across sites and across years but even the lowest of the estimated rates would lead to >80% of marmots being detected in a 3-day sampling period.

There was generally high concordance between MNA and $\hat{N}$ ($r = 0.94$, $n = 32$, $P < 0.001$; Fig. 4), although the MNA estimate on average detected one marmot more than $\hat{N}$. This discrepancy often occurred when marmots died shortly before the resightings, particularly in the spring when the resighting was late in the ~2-month period used to determine MNA.

Population growth rates

Most (11 of 16) estimates of population growth rate based on the time-series, and all projections based on matrix models, indicated that the marmot populations in our three study areas are declining (Fig. 5). At the Western sites the matrix model, parameterized with five years of demographic rates, predicts a population declining at 12% per year. This rate of decline is greater than that of the estimates obtained from the trend data but within 1 standard error of three of the four of those estimates. For the Central sites, the matrix models project a population declining by 8% per year, a rate very close to that observed in the time series at the large Central-A site group. For Royal Basin the projected annual decline of 2% is not as severe as that detected in the population trends but again falls within 1 standard error of the observed trends. To determine the effect that the likely overestimate of subadult apparent survival might have had on the projected growth rate at Royal Basin, we decreased subadult survival from 0.89 to 0.75 in the matrix model. This resulted in a projected 5% annual decline in population size, which although still less severe than the declines indicated by the trend data, represents a sharply declining population.

Discussion

Multiple lines of evidence all indicate that Olympic marmots have undergone local and range-wide declines over the last $10 - 15$ years. In the northeast, marmots have disappeared from several areas where there was evidence of continuous occupancy for > 40 years, and current population trends and demographic rates indicate that the declines are ongoing in extant population. While the strongest and most dramatic evidence comes from the northeast, similar or higher ratios of abandoned to occupied habitat in other

regions suggest that the declines are a widespread phenomenon. Few historical records of marmots exist in the southwest and there is sparse physical evidence of current or recent occupation, so it is plausible that habitat density or quality in that region is and has been too low to support a substantial marmot population. The southeast, where the ratio of abandoned to occupied habitat is even higher than in the northeast, may warrant particular concern.

These apparent declines are particularly troubling given the precarious status of the nearby and taxonomically similar Vancouver Island marmot population, which crashed to near extinction in the 1990's and would likely have gone extinct if not for an intensive captive breeding program. Changes in the abundance and distribution of predators resulting from industrial forestry appear to have played a considerable role in the decline of that species (Bryant 1998). Although the forests within the park are relatively pristine, predator-prey dynamics on the peninsula have been altered by the extirpation of the wolf (*Canis lupus*) from the peninsula in the early 20th century and the simultaneous arrival of the coyote (*C. latrans*) , industrial forestry and residential development outside the park, and current and historic ungulate hunting practices. That both marmot species evolved on actual or effective islands in the absence of many mainland predators and competitors, and both have probably never numbered more than a few thousand, suggests that each could be particularly vulnerable to novel predators or significant changes in predator abundance. The striking similarities in the demographic performance of the Olympic and Vancouver Island marmot populations – both species currently have very low survival of non-juveniles and similar juvenile survival and

reproductive rates (A. A. Bryant and S. C. Griffin, *unpublished data*) – suggest that the Olympic marmot may be headed the way of the Vancouver Island marmot.

Distinguishing declines from metapopulation processes

Marmots have been postulated to exhibit classic metapopulation dynamics (Bryant & Janz 1996; Ozgul et al. 2006) and any evaluation of status that relies on occupancy rates must consider whether the observed occupancy patterns represent equilibrium background extinction and colonization patterns. A qualitative analysis of the spatial and temporal distribution of the observed extinctions and recolonizations, dispersal patterns, and demographic rates in the context of other stable and declining populations of marmots all suggest that this is not the case.

First, the spatial patterns of the Olympic marmot extinctions are unlike the long-term patterns in an apparently stable yellow-bellied marmot metapopulation (Ozgul et al. 2006), although both populations consist of groups of nearby sites (termed "networks" by Ozgul et al.) consisting of several large or high-quality patches and additional smaller or lesser quality patches (Fig. 6). Many of the larger yellow-bellied marmot colonies have been continuously occupied for >40 years (Blumstein et al. 2006), and the estimated annual local extinction probability drops off rapidly with local population size (Ozgul et al. 2006). This is consistent with apparent Olympic marmot extinction and colonization processes from 1957 – 1989, a period in which occasional extinctions and colonizations of the smallest sites occurred but the larger colonies appear to have been persistent (Table 1). Simulations demonstrated that overall population persistence is sensitive to extinctions of colonies where the population size of adult females averages >1 and to the

extinction of individual networks (Ozgul et al. 2006). These features highlight the importance of larger sites as a source of colonists and of inter-network movement for maintenance of the overall population.

In contrast to the pattern of persistent large patches maintaining networks of sites reported by Ozgul et al. (2006), all or most of the colonies within some individual networks of Olympic marmot sites have become extinct, with little regard to colony size. This has predictably led to increased isolation of the remaining sites and presumably increased their extinction risk. For example, historically there were ≥ 5 sites that averaged > 1 adult female in the vicinity of the Hurricane Ridge Visitor Center (Barash 1968, 1973) – these would have fallen within our Western site group. With the extinction of these and the adjacent smaller sites, Hurricane Hill has become very isolated (> 10 km from any colony > 5 marmots) and seems likely to succumb to stochastic events. Four tiny sites (2-4 marmots) on Mt. Angeles also seem unlikely to persist in the absence of support from the now-extinct sites. Similarly, the vacant sites on Blue Mountain included at least two relatively large, persistent marmot colonies and several smaller ones. The nearest potential source of colonist (i.e., a site currently occupied by > 5 marmots) is now > 8 km from Blue Mountain. Numerous other examples of "network" extinctions appear to exist in other regions of the park and many of the remaining networks are becoming increasingly isolated.

A second reason why current occupancy patterns are not representative of equilibrium metapopulation dynamics is that Olympic marmot dispersal patterns appear to severely limit the probability of widespread recolonizations. While the majority of yellow-bellied marmots of both sexes disperse as yearlings (Schwartz et al. 1998; Van

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Vuren 1990), and other marmot species are known to move long distances (Van Vuren & Armitage 1994, A. A. Bryant, personal communication), movement of Olympic marmots appears to be more limited. We have no record of any untagged marmot migrating onto any of our study sites during the 4-5 years of study. Among the 101 radio-tagged animals, only nine attempted to migrate off the site where they were initially tagged. Of these, six successfully settled 0.5 - 1 km from the initial site, one traveled 2.5 km before returning to the natal colony, and two traveled 4.5 - 6 km before being depredated. Additionally, two ear-tagged marmots successfully dispersed distances of < 0.8 km and 2.5 km. Of the eight animals known to have dispersed successfully, only two were female. Sherman and Runge (2002) reported a similar lack of movement among ground squirrels colonies during a severe population collapse.

Finally, current Olympic marmot mortality rates, particularly those of adult females at the Western and Central site groups, are more similar to (although slightly lower than) the endangered Vancouver Island marmot (Bryant and Page 2005, A. A. Bryant and S. C. Griffin, *unpublished data*) than they are to rates recorded for Olympic marmots in the 1960's (Barash 1973). Population growth rates for long-lived, late-maturing species are known to be sensitive to changes in the survival rates of adult females (Heppell et al. 2000; Oli & Dobson 2005) – the low projected population growth rates are consistent with this. In addition, the slightly reduced reproductive rates in the current population may be a secondary effect of the high female mortality rates. The most parsimonious explanation for the consistently high mortality of adult females in June would be that they are more vulnerable to predation due to pregnancy or lactation (e.g.,

Hoogland et al. 2006), and several of the females that were killed in this period were known or suspected to be pregnant or lactating.

It is also important that both the proximate and ultimate causes of the declines be identified (Sherman & Runge 2002). The widespread distribution of the abandoned sites supports earlier findings that direct human disturbance is probably not responsible (Griffin et al. 2007b). Similarly, we saw no indication of disease in the ≥ 200 marmots we handled and ≥ 100 examined by a veterinarian. Overwinter survival was high, reproductive rates were in the expected range, and body condition was good (data not shown), suggesting that neither forage quality nor overwinter conditions have been degraded by climate change, although they may be in the future. The high mortality of adult females at two of three site groups suggests that predation is the proximate cause of the immediate declines. It is possible, however, that the population may have become more vulnerable due to landscape level changes in meadow distribution, as has been proposed for the Idaho ground squirrel (Sherman & Runge 2002). Aerial photos of the Hurricane Ridge area taken in 1939 and 2000 show substantial increase in tree cover during that period, although the net change in high-elevation meadows across the park is unknown. If forest cover did increase over the last century due to climate change or fire suppression, the result would have been increasing isolation and decreasing size of suitable meadows. This would have led to a decreased frequency of successful dispersal events, improved cover for terrestrial predators, and possible Allee effects resulting from smaller groups of marmots.

Management recommendations and research needs

We recommend implementing a range-wide monitoring program that takes into consideration the role of local networks of sites in population persistence, and continuing to monitor abundance and demographic rates at a subset of sites. Although occupancy monitoring is financially and logistically more feasible than demographic monitoring, the age and sex bias in mortality rates could lead to a time lag between functional declines and numerical declines or site abandonment. Only by identifying geographic regions where marmots are currently declining can management possibly arrest or reverse the situation. Management efforts would also benefit from a reliable estimate of current population size. An earlier estimate of 2000 Olympic marmots (Barash 1989b) appears to have originated in a 1918 Forest Service report (Sheffer 1995). We believe the number of marmots is actually ≤ 1000, but this estimate is tenuous as well due to the wide range of marmot densities, which often appear to be unrelated to habitat characteristics, and the difficulties associated with assessing population size of unmarked animals at remotes sites.

Conclusions

Uncertainty is often an unavoidable component of ecological research. Assessments of the status of small, scattered, populations in remote landscapes will almost always involve some degree of uncertainty. Alone, no one of the four lines of evidence that we presented would absolutely demonstrate that Olympic marmots are in a sustained decline across their range. However, each is consistent with such a decline, while the spatial pattern of the extinctions is inconsistent with metapopulation dynamics of a population at equilibrium. In effect, by considering multiple metrics of distribution and demography, as well as how the observed patterns compare to those seen in other

species of marmots, we have reduced the uncertainty about Olympic marmot population status to a negligible level.

Table 1. Occupancy data for 25 colonies of Olympic marmots (*Marmota olympus*) in Olympic National Park 1957-2006. "P" indicates that marmots were determined to be present in a given year, "A" indicates that they were absent, and blanks indicate that no data are available. No. corresponds to locations shown in Fig. 1. Sources are indicated in footnotes below the table. The codes in the access column refer to the location and study intensity of the site (d, demographic study site; vc, located adjacent to Hurricane Ridge Visitor Center and surrounding paved walking paths; t, adjacent to popular hiking trail; r, adjacent to road; ol, visible from popular overlook.

Table 2. Reproductive and survival rates for Vancouver Island marmots, historic populations of Olympic marmots, and 2002-2006 Olympic marmots at three site groups. For litter size, the mean, with sample size and SD in parentheses, is shown. For all other rates, the sample size, and upper and lower 95% confidence limits are given. For the adult and subadult survival rates, sample size – representing the number of individuals considered – is followed by the number of 0.5-month active season intervals in square brackets. The proportion of Olympic marmot females reproducing in the current study differed among sites groups ($X_2^2 = 6.13; p < 0.05$). Other rates were similar among site groups in the current study, based on X^2 or one-way ANOVA as appropriate.

No.	Colony	access	1957[1]	1966[2]	1967[3]	1968[3]	1969[3]	1972[4]	1975[5]	1989[6]	1996[7]	2002[8]	2003[8]	2004[8]	2005[8]	2006[8]
Hurricane Ridge Visitors Center Area																
1	Bartholomew (Sunrise Basin)	d, r		P	P	P	P			P		P	A	A	A	A
2	Widow (Sunrise Basin)	d, r			P	P	P	P		P	P	P	A	A	A	A
3	Meander	t			P	P	P			P		A	A	A	A	A
4	Marigold	t			P	P	P	P	P	P		A	A	A	A	A
5	Henderson	vc		P	P	P	P			P		A	A	A	A	A
6	Henderson Annex	vc			A	P	P			P		A	A	A	A	A
7	Lodge	vc		P	P	P	P			P		A	A	A	A	A
8	Picnic	d, t	P	P	P	P	P	P		P	P	P	P	P	P	P→A†
Hurricane Hill Area																
9	Agean/Hurricane Hill Elwha	d, t				P	P					P	P	P	P	P
10	Cornus	d	P		P	P	P			P		P	P	P	P	P
11	Ridgely	d	P			P	P	P		P	P	P	P	P	P	P
12	Allee	d				P	P			P	P	A	A	A	A	A
13	Zenith	d, t					P				P	P	P	P	P	P
Obstruction Point Road & vicinity																
14	Aureus (Eagle Point)	d, r	P	P	P	P	P	P		P		P	P	P	P	P
15	Aureus Annex	r			A	A	P			P		A	A	A	A	A
16	Steeple	r	P		P	P	A			P		A	A	A	A	A
17	Badger Valley	t	P					P		P		P	P	P	P	P
18	Elk Mountain	t						P		P	P	P	P	P	P	P
19	Swimming Hole			P				P				P	P	P		P

[1] (Meagher 1957)
[2] (Barash 1968)
[3] (Barash 1973)
[4] (Wood 1973)
[5] (Watson 1976)
[6] (Houston et al. 1994b)
[7] Blumstein, D. T. pers. comm.
[8] This study.
† This colony became extinct during summer 2006.

Royal Basin

#	Location													
20	Royal Basin West	d					P	P	P	P	P	P	P
21	Royal Basin East	t					P	P	P	P	P	P	P

Blue Mountain

#	Location													
22	Large basin east of Blue Mountain summit	ol	P					P	A	A	A	A	A
23	Thistle	t	P	P	P	P		P	A	A	A	A	A
24	Rocky ridge south of eastmost switchback above campground	t	P					P	A	A	A	A	A
25	Slope north of rocky ridge and south of basin	t	P					P	A	A	A	A	A
	Blue Mountain – unspecified			1951[9], 1955[9], 1963[9], 1964[9], 1983[10]					A	A	A	A	A

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[9] Voucher specimens collected by M. L. Johnson, housed at the University of Puget Sound, Slater Museum, 1500 North Warner St., Tacoma, WA 98416.

[10] J. Burger, Olympic National Park Education Division, personal communication

Demographic rate	Vancouver Island marmots[11]	Olympic marmots				
		Historic[12]	Hurricane Hill	Obstruction Point	Royal Basin	All colonies
Females reproducing	0.41 (134; 0.33, 050).	0.41 (59; 0.28, 0.54)	0.38 (24; 0.19, 0.59)	0.48 (44; 0.32, 0.63)	0.21 (34; 0.09, 0.38)	0.36 (102; 0.27, 0.46)
Litter size	3.38 (58; 1.14)	4.04 (24; 1.20)	3.22 (9; 1.39)	3.33 (18; 1.08)	3.50 (2; 0.71)	3.31 (29; 1.14)
Sex-ratio (proportion female)	0.51 (108; 0.41, 0.61)		0.55 (11; 0.23, 0.83)	0.59 (44; 0.43, 0.74)	0.5 (4; 0.68, 0.93)	0.58 (59; 0.44, 0.70)
Juvenile survival (from emergence)	0.53 (75; 0.42, 0.65)	0.55 (64; 0.40, 0.66)	0.63 (24; 0.41, 0.81)	0.57 (58; 0.43, 0.70)	0.71 (7; 0.29, 0.96)	0.60 (89; 0.49, 0.70)
Juvenile survival (from tagging)			0.65 (20; 0.41, 0.85)	0.64 (53; 0.50, 0.77)	0.80 (15; 0.52, 0.96)	0.67 (88; 0.56, 0.77)
Adult female survival (annual)	0.76 (- [-]; 0.68, 0.83)	0.89	0.62 (11 [181]; 0.47, 0.75)	0.62 (18 [187]; 0.47, 0.75)	0.80 (11 [205]; 0.61, 0.91)	0.69 (40 [573]; 0.58, 0.78)
Adult female survival (to July 15)	0.96		0.78 (11 [99]; 0.66, 0.91)	0.78 (14 [83]; 0.66, 0.91)	0.89 (10 [91; 0.79, 0.99])	0.83 (35 [273]; 0.72, 0.93)
Adult male & subadult survival	0.76 (- [-]; 0.68, 0.83)		0.78 (24 [282]; 0.69, 0.85)	0.78 (40 [482]; 0.69, 0.85)	0.89 (18 [148]; 0.75, 0.96)	0.79 (82 [912]; 0.72, 0.85)
Projected r			-0.12	-0.08	-0.01	-0.07

[11] Vancouver Island marmot reproductive rates reported for wild marmots in Bryant (2005), juvenile survival through 2004 from A.A. Bryant (personal communication). Adult survival rates from Bryant and Janz (2005); it was not possible to determine sample sizes of the appropriate non-juvenile age and sex classes from this reference.
[12] Historic Olympic marmot rates from Barash (1973; table 3). Data therein are insufficient to determine female survival to July 15.

Figure 1. Location of survey polygons within Olympic National Park where Olympic marmots (*Marmota olympus*) were detected (open squares) and those polygons that appeared to have been occupied by marmots in the recent past (open circles) during surveys conducted in 2002-2006. Gray shading indicates those areas predicted to be suitable habitat. The nine sites where marmots were marked and monitored are shown in the inset as follows: 1) Hurricane Hill; 2) Sunrise Basin; 3) Picnic; 4) Eagle Point; 5) Pull-out; 6) Marmot Flats; 7) Obstruction Point; 8) Pumpkin Seed Lake; and 9) Royal Basin.

Figure 2. Entrance mound outside a typical Olympic marmot burrow. These mounds are formed from excavated dirt and are either directly downslope from or surrounding the entrance hole. Large mounds can often be detected at a distance due the bright green sedge (*Carex spectabilis*) surrounding the compacted dirt porch.

Figure 3. Proportion of occupied, abandoned, and no sign polygons in Olympic marmot habitat survey differed by geographic region. See Figure 1 for delineation of regions.

Figure 4. Abundance of Olympic marmots age $\geq$ 1 year at intensive study sites 2002 – 2006 (by site group), with projected maximum abundances for spring 2007. MNA represents the number of animals detected by any means during the spring (May and

June) or fall (August and September) of each year. N-hats, with 95% confidence intervals, are estimates from mark-resight data.

Figure 5. Estimates of the mean intrinsic growth rate ($\hat{r}$) for each site group for spring and fall based on mark-resight estimates (CMR) and minimum number alive (MNA) in each period, and based on a group specific deterministic matrix model. Error bars represent 1 SE of the estimates. The regression method (Dennis et al. 1991) was used to obtain the estimates, with 1 -5 intervals per site / season / method combination. The last data point used in spring MNA regressions is the expected maximum value for spring 2007, based on marmots known alive in fall 2006. See Figure 4 for specifics on sampling intervals and data points used.

Figure 6. Distribution of current and known historic Olympic marmot colonies on the northern ridge system in Olympic National Park. The Central and Western Colonies occupied as of fall 2006 are shown with black symbols, historically occupied colonies that were vacant by 2002 are shown with hollow symbols, and colonies (Picnic and Sunrise Basin) that became vacant since 2000 are shown with gray fill. Symbol size corresponds to number of breeding age females typically supported by the site ($\leq 1, > 1 - 2, > 2$). Number of breeding age females was determined from data collected in this study or by Barash (1973) or was estimated based on meadow size and burrow density at sites where no data are available. Sites where average number of females was known are with diamonds and those for which we estimated size are shown with squares.
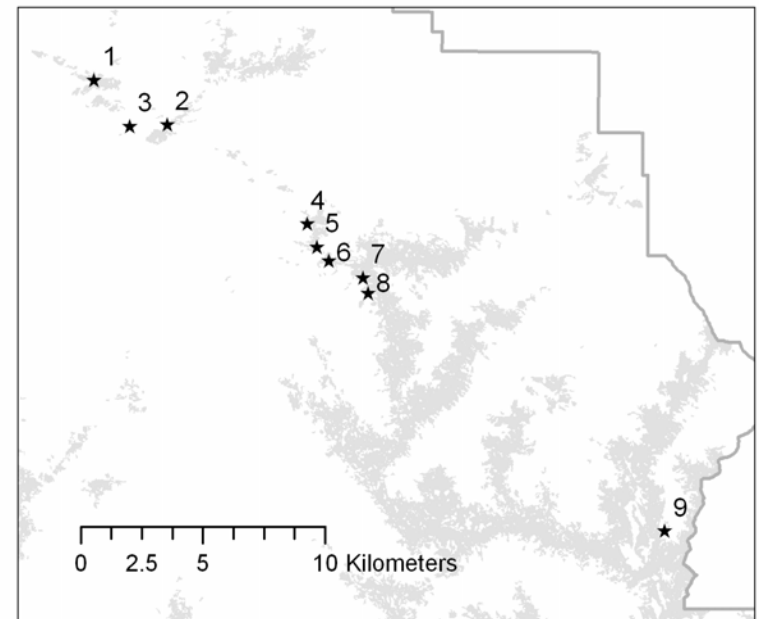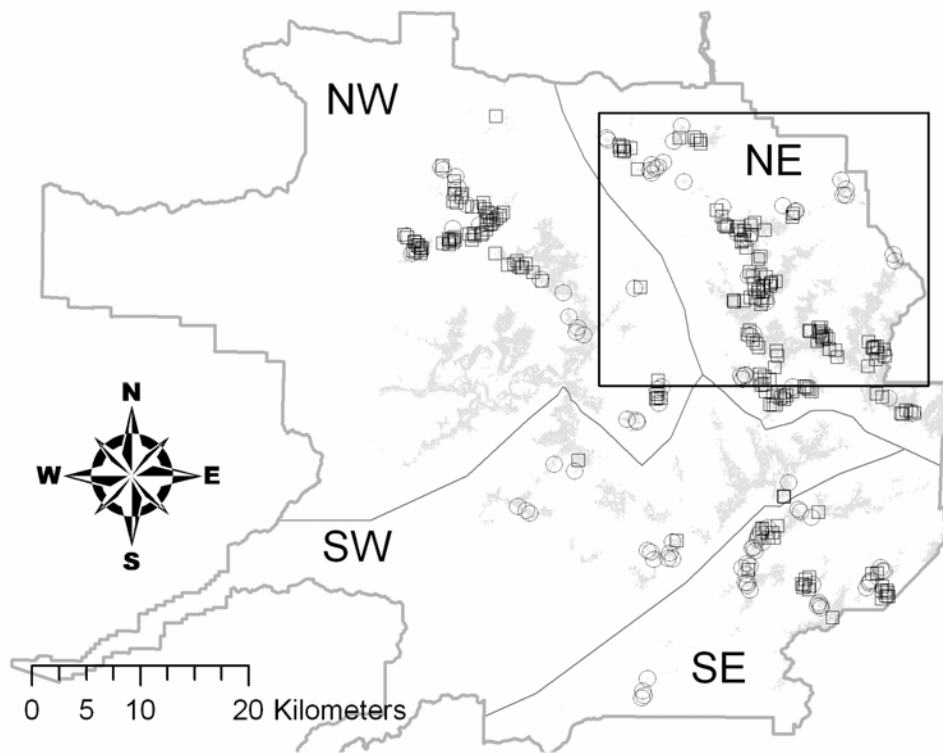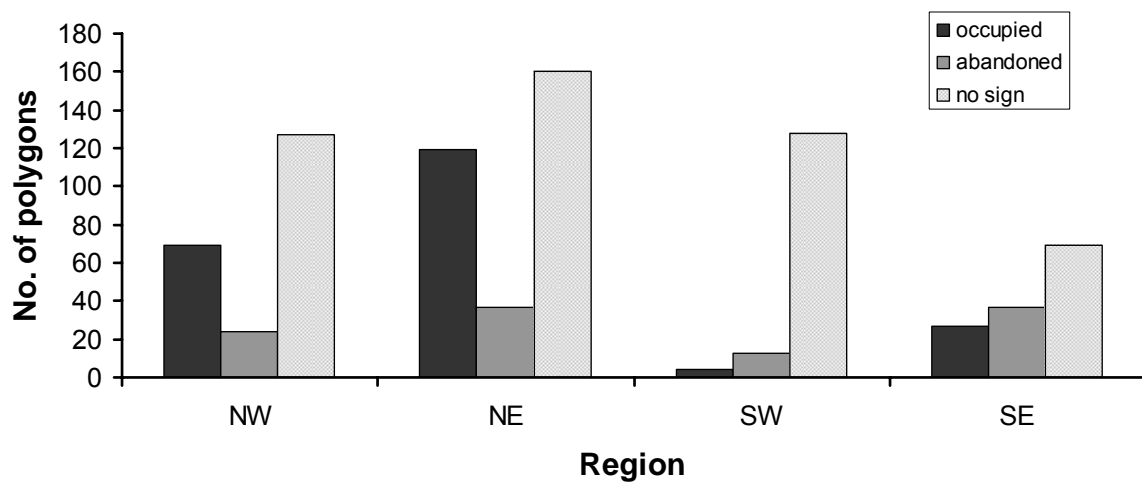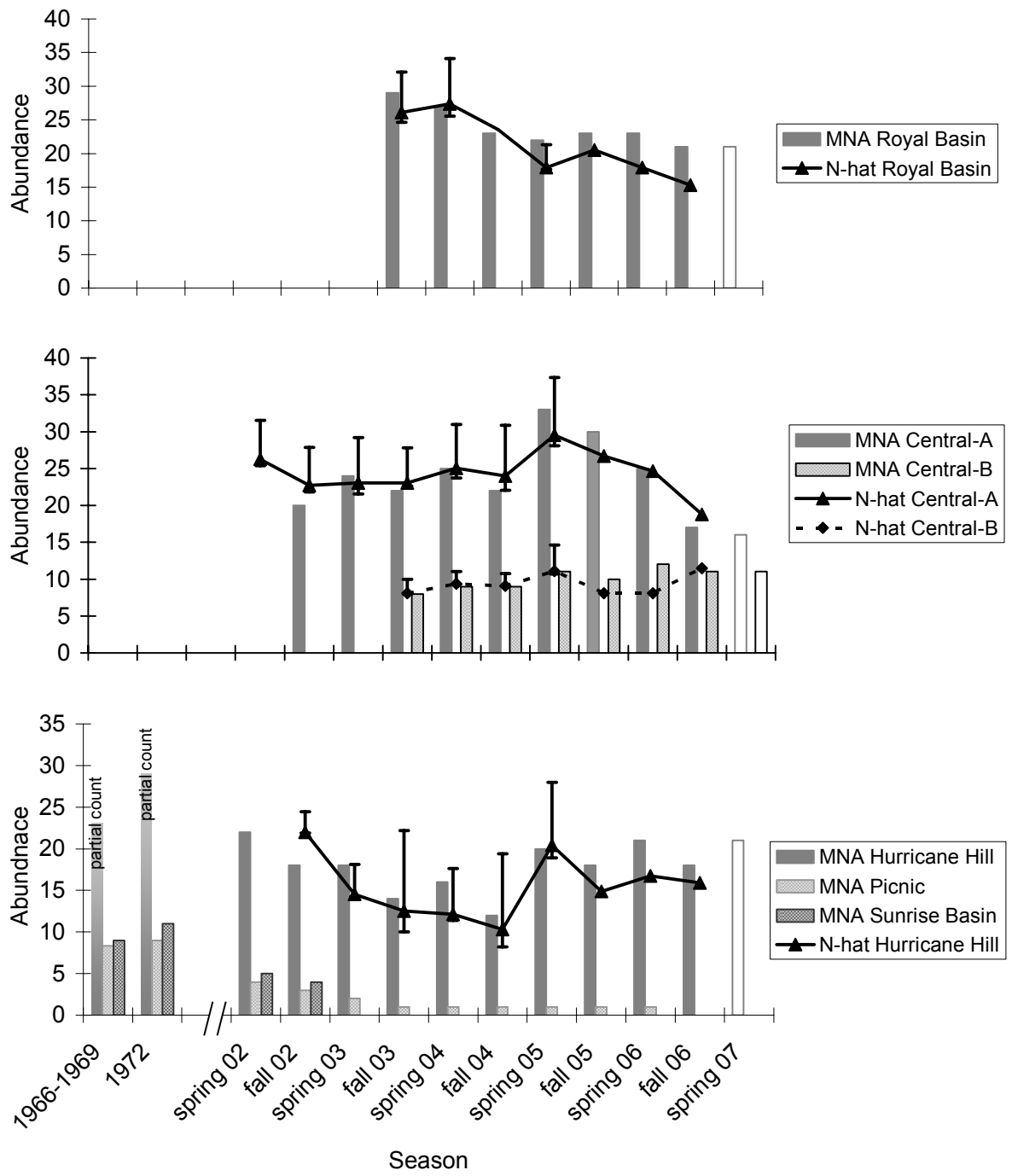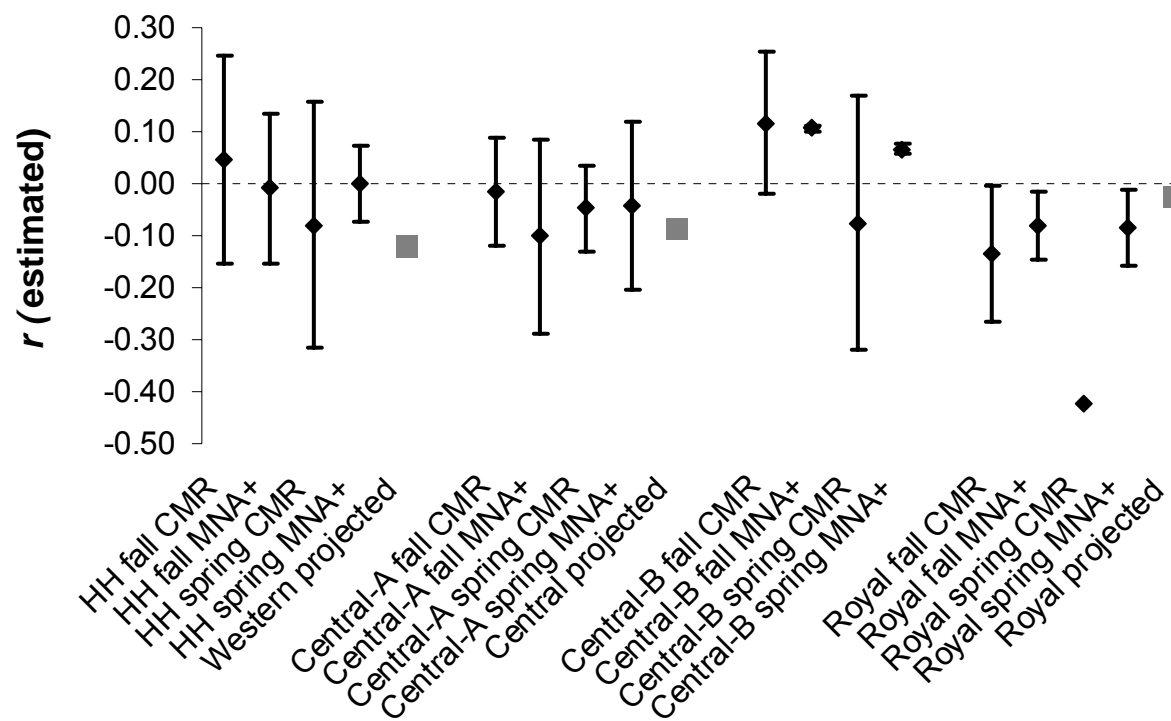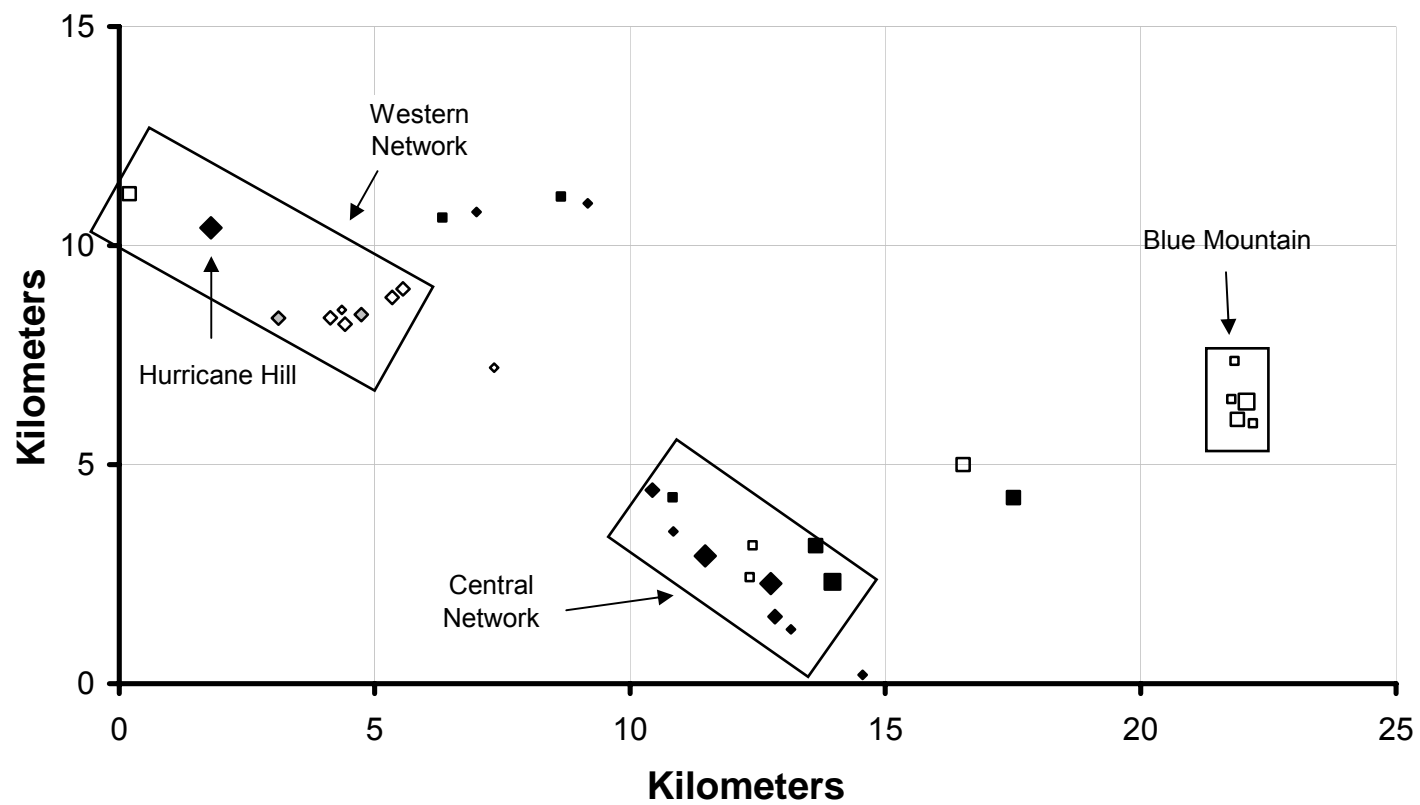
CHAPTER 2.

EFFECTS OF TOURISTS ON BEHAVIOR AND DEMOGRAPHY OF OLYMPIC MARMOTS

Abstract: If changes in animal behavior resulting from direct human disturbance are to negatively affect the persistence of a given species or population, these behavioral changes must lead to reduced demographic performance. We tested for effects of human disturbance on Olympic marmots (*Marmota olympus*), a large ground-dwelling squirrel that has disappeared from several areas where recreation levels are high. We assessed the degree to which antipredator and foraging behavior and demographic rates (survival and reproduction) differed between sites with high recreation levels (high use) and those with little or no recreation (low use). Compared with marmots at low-use sites, marmots at high-use sites displayed significantly reduced responses to human approach, which could be construed as successful accommodation of disturbance or as a decrease in predator awareness. The marmots at high-use sites also looked up more often while foraging, which is suggestive of increased wariness. Marmots at both types of sites had comparable reproductive and survival rates and were in similar body condition. Until now, the supposition that marmots can adjust their behavior to avoid negative demographic consequences when confronted with heavy tourism has been based on potentially ambiguous behavioral data. Our results support this hypothesis in the case of Olympic marmots and demonstrate the importance of considering demographic data when evaluating the impacts of recreation on animal populations.

Introduction

Hiking, wildlife observation, and other nonconsumptive outdoor recreation can have considerable influence on the behavior and distribution of wild animals (e.g., Constantine et al. 2004; Finney et al. 2005; Klein et al. 1996). Changes in behavior and distribution have the potential to translate into fitness costs. However, the demographic effects of avoidance or habituation behavior are not always obvious, and truly informed management can occur only if the impacts of recreation on a population's vital rates are known (Gill et al. 2001). Unfortunately, such demographic data are often lacking; thus, management recommendations are made based solely on behavior and distribution changes (e.g., King & Heinen 2004; Klein et al. 1996; Papouchis et al. 2001), leaving the potential for unnecessary (and unpopular) restrictions on recreation if impacts are overestimated.

Alternatively, the true cost of disturbance may be underestimated, particularly in species that manifest few overt responses to human disturbance. Species with limited ability to move away from disturbance could suffer a high demographic cost and so be particularly vulnerable (Gill et al. 2001). Similarly, one life stage or age class may be affected negatively by disturbance, whereas while another may be unaffected or appear to habituate. In one of the few studies that has explored demographic costs of disturbance, Müllner et al. (2004) found that adult Hoatzins (*Opisthocomus hoatzin*) habituate to regular tourism but that similarly exposed juvenile birds exhibited increased hormonal stress responses, reduced body mass, and ultimately, lower survival than those at undisturbed sites. Other apparently habituated animals display altered hormonal and behavioral responses to simulated (and possibly real) threatening situations. Magellanic

Penguins (*Spheniscus magellanicus*) habituate after only a few visits, but highly disturbed birds have a reduced capacity to secrete corticosterone – the long-term effects of which are unknown (Walker et al. 2006). Finally, even where habituation does not result in physiological or behavioral changes, tolerance is unlikely to be absolute (Frid & Dill 2002). Animals continue to flee from some tourists and expend time and energy monitoring those outside the flight zone. Without demographic data, the true costs of these responses cannot be evaluated.

The impact of human disturbance on alpine-dwelling members of the genus *Marmota* is a concern because recreation in their habitats has increased. These large ground-dwelling squirrels inhabit alpine and subalpine meadow throughout the northern hemisphere (Armitage 2003). Their narrow habitat requirements and dependence on a complex burrow system prevent them from moving away from an area if conditions deteriorate. Similarly, they cannot temporally avoid tourists because they are diurnal and must forage extensively during the short alpine summer – when tourism is highest. Most marmot species have been hunted (Armitage 2003), sometimes intensively, for millennia and thus would be expected to respond to humans as a threat (Frid & Dill 2002).

The Olympic marmot (*Marmota olympus*) is endemic to subalpine meadows on the Olympic Peninsula in Washington State (U.S.A.). Their habitat lies almost entirely within Olympic National Park, where they are viewed by thousands of park visitors. In the last 15 years, Olympic marmots have declined or disappeared completely from several locations that had been continuously occupied for at least 40 years (S.C.G., M.L.T, and L.S.M., unpublished data). Human activity levels are high in some of these

areas. It is unknown whether the locations of the known declines are related to recreation or are an artifact of historic sampling effort.

Most evaluations of the impacts of nonconsumptive recreation on fossorial sciurid rodents (prairie dogs [*Cynomys* spp.], ground-squirrels [*Spermophilus* spp.], and marmots) have been limited to examining warning and flight responses of animals that frequently encounter hikers relative to those that do not. Alpine marmots (*M. marmota*) inhabiting popular hiking areas and prairie dogs (*C. ludovicianus*) in urban parks both exhibit reduced flight distance in response to predictable human actions (Louis & Le Berre 2000; Magle et al. 2005; Neuhaus & Mainini 1998), although with repeated direct approaches, prairie dogs increase their reaction distance (Magle et al. 2005). It has been postulated that the increased tolerance to close human approach indicates that marmots can adjust their behavior to accommodate human presence, avoiding demographic costs (Louis & Le Berre 2000; Neuhaus & Mainini 1998). Conversely, reduced flight distance may be synonymous with generally reduced wariness (Blumstein et al. 2001), and it is unknown whether habituation is accompanied by physiological changes in stress response as seen in other species (Walker et al. 2006). Mainini et al. (1993) found that habituated marmots react more strongly to a hiker with a dog than to one without, suggesting that the predator response is present, but no comparison was made with undisturbed animals, so it remains unclear whether the response of regularly disturbed marmots is dampened. Others have investigated space use and burrow distribution within the home range (Franceschina-Zimmerli & Ingold 1996; Semenov et al. 2002) and time budgets (Louis & Le Berre 2002) when human disturbance is high. However, these studies were unreplicated and did not investigate demographic responses to tourism. Several sciurid

species are listed as threatened or endangered by state, provincial, or federal governments (e.g., Vancouver Island marmot [*M. vancouverensis*]; Mexican prairie dog [*C. mexicanus*]), and these animals are often found in recreation areas.

We used recreation level at different marmot colonies as a treatment in a natural experiment to assess whether visitors are having a negative impact on extant Olympic marmot colonies. We first determined the degree to which multiple antipredator and foraging behaviors of Olympic marmots differ between heavily visited and relatively unvisited sites. Because the importance of observed behavioral differences were not immediately obvious, we then used existing data to determine whether survival and reproductive rates were lower at the heavily visited sites.

Methods

Study Area

Olympic marmots inhabit scattered meadows above 1400 m throughout Olympic National Park (ONP) and surrounding Olympic National Forest. Over 3 million people visit ONP annually, with June – August being the most popular months (National Park Service 2005). Three roads allow summer access into the high country. Hiking and backpacking occur throughout ONP but high-country use is heaviest near these roads. Marmots currently inhabit meadows adjacent to, and even bisected by, the Obstruction Point Road. Until recently, marmots also occupied meadows surrounding a large parking lot on Hurricane Ridge.

Behavioral-Observation Sites

Behavioral experiments and observations were made on 1 or 2 days in 2004 at each of seven heavily visited sites (high use) and six undisturbed (low use) sites (Table 1). For the purpose of this study, a site is a meadow occupied by one family group or interacting family groups of marmots. Randomly assigning sites to receive different levels of tourist pressure was not possible. Instead, we minimized the confounding effects of other factors by observing behavior at multiple sites for each visitation level. We selected behavioral sites so that we could compare naïve marmots with those that were heavily exposed to humans.

We chose seven high-use sites from among those with the greatest levels of human visitation among extant marmot colonies. These seven sites represented a range of human activity types (car, hiker, or campsite) and geographic distribution. Marmot colonies at these sites were bisected by or adjacent to a heavily used trail, road, or designated high-use campsite. As a coarse index of human use, hikers and cars (collectively, tourists) were counted during a single morning or in both the morning and afternoon at each site. One or more hiker groups or tourist cars were seen at each of the seven high-use sites during the morning (0700 – 1300 hours; Table 1). Cars or hikers appeared to be visible to a focal marmot for an average of 27 minutes (7.7%) of the 6-hour period (Fig. 1). At three of the high-use behavioral sites, cars and hikers were also counted in the afternoon (1300 – 2000) and appeared to be visible to the marmots for an average of 64 minutes, or 15.3% of that 7-hour period. This is consistent with our impression that human disturbance is greater in the afternoon. Since 2002, we have conducted trapping and radiotelemetry work at three high-use sites (Eagle Point, Marmot

Flats, and Obstruction Point). We always conducted behavioral observations at least 5 days after any trapping operations to avoid aftereffects of our activities.

The six low-use sites were generally >100 m from any trail, road, or campsite and not visible from areas regularly used by tourists. These sites were identified in the course of extensive ground surveys in 2002 and 2003 (S.C.G., M.L.T., and L.S.M., unpublished data) but were not visited in 2004 prior to the behavioral observations. We did not see any humans at the low-use behavioral sites during our observations.

Demographic Sites

We used data (collected in 2002-2005 as part of a separate study) from marked marmots at 11 sites to compare reproductive rates, survival, and body condition among marmots at sites that had heavy human traffic (high use; $n = 7$; Table 2) in the form of hikers, cars, or both and at sites that were largely undisturbed (low use, $n = 4$). We conducted trapping and telemetry operations several days each year at each of these sites. These activities may have influenced the marmots' behavior, but it is not possible to gather detailed demographic data without disturbing the animals. To confirm that the effect of our disturbance was minimal, we compared behavioral data from three of the four low-use demographic sites (Royal Basin, Pumpkin Seed Lake, and Jon's Basin) with data from low-use behavioral sites. Not all demographic sites were studied in all years. Marmots did not persist at Hurricane-Elwha Junction after June 2003, and we added sites in 2003. We did not include data from several colonies that had intermediate levels of disturbance.

Behavioral Observations

We conducted observations at the 13 behavioral sites in clear or partly cloudy

weather between late-June and late-August 2003 (Table 1). Observations at both high-

and low-use sites were distributed similarly throughout summer ($n = 13$; Mann-Whitney

U statistic = 15.5; $p = 0.431$). Likewise, sites had similar numbers of marmots ≥ 1 year

old (infants appear above ground in late-July) present at the time of sampling ($n = 13$; U

= 12.5; $p = 0.212$). Through the use of multiple sites of each type, we attempted to

minimize the effects of site-specific conditions such as topography or recent predation

events on marmot behavior. The same observer (T.V.) made all observations and

experiments except those at Swimming Bear Lake, which were done by an observer

trained by T.V. The distance between the observer and the focal marmot was never < 50

m and usually > 100 m.

Looking-Up and Flight Behavior

The vigilance behavior during foraging, as measured by the frequency (number of

looks), average duration (average look), and total time the animal devoted to looking up

(total time looking), was observed for two or three adult (≥ 2 years old) animals per site

generally following the methods of Blumstein et al. (2001). Specifically, once a focal

animal had been foraging for several minutes, we noted, on a handheld tape recorder,

each time the marmot looked up and then back down during a 2.5-minute period. The

first 0.5 minutes of tape were not used in the analyses to reduce biases associated with the

timing of initiation of the observation period. For comparison with low-use sites,

observations at high-use sites were made while no tourists were present. Easily

recognized marmots (distinctive molt pattern) were chosen for observation to avoid using

the same animal twice. In each case, the number of other marmots (foraging group size)

apparently visible to the focal animal during the observations was noted because

vigilance may be affected by group size (Blumstein 1996; Blumstein et al. 2004). One

person (T.V.) transcribed all tapes with a stopwatch used to measure time between each

word *up* and *down*.

We evaluated the relative sensitivity of marmots to a potential predator by

measuring how close a human, walking at a constant pace across the slope directly

toward a foraging marmot, could get to the animal before it ran to a burrow (flight

distance) and subsequently went below ground (ground distance) and by measuring how

long the marmot remained in the burrow after the human moved away (exit delay). The

distance of the marmot (distance to burrow) from its burrow at the start of the experiment

was also recorded because this distance can influence flight distance (Bonenfont &

Kramer 1994). All distances were measured with a laser range finder. Three marmots on

each site were tested, with ≥ 30 minutes between the culmination of the experiment on

one animal and the beginning of the experiment on the next. We conducted all flushing

experiments after collection of observational data.

Activity Budget

To assess the amount of time marmots devoted to foraging and vigilance, we

compiled a morning activity budget for one adult marmot at each of the 13 sites. We

watched the first readily identifiable marmot from its initial emergence in the morning

until it reentered its burrow and remained there for at least 1 hour after 12:00 hours. In no

case did a marmot fail to remain in the burrow for at least 1 hour in the early afternoon.

We restricted our observations to the morning activity period because heavy rain or

extreme heat in the afternoon frequently caused the marmots to remain inactive for several hours (Barash 1973; Melcher et al. 1990).

We continuously monitored the behavior of the focal animal, recording the time that a change in activity occurred. For analysis, activities were classified as below ground; foraging (including brief instances of looking up, ≤ 10 seconds); vigilance (any instance of looking up > 10 seconds, typically while sitting or lying at the burrow entrance or on a rock); traveling; and other (social, grooming, and other miscellaneous activity). A sixth activity (lying without looking around) was measured but not considered because it averaged < 1% of a marmots' morning activity. When a marmot at a visited site went below ground, we noted whether the animal appeared to be fleeing a human or whether it did so of its own volition.

Demographic Observations

Trapping and Implantation of Radio-transmitters

As part of an ongoing study, all marmots at the 11 demographic sites had been marked and monitored since 2002 or 2003, and a subset had radio-transmitter implants (Table 2). We generally followed trapping and handling procedures outlined in Bryant (1996), with two exceptions: we used xylazine in addition to ketamine to sedate the marmots and we attached one or two small (<1 cm) pieces of colored wire to each tag to facilitate recognition of individuals without recapture. Most subsequent recaptures were identified, weighed, and released.

We surgically implanted 40-g radio transmitters in the peritoneal cavity of 62 marmots ≥ 1 year old, following published surgical methods (Bryant & Page 2005; Van Vuren 1989). Intraperitoneal transmitters have been widely used in studies of marmots

with no detectable reduction in survival or reproduction (Bryant & Page 2005; Griffin et al. unpublished data; Van Vuren 1989). We never trapped or resighted a marmot with a failed transmitter, but we did replace five transmitters as they neared the end of the expected battery life.

Survival and Reproduction

We confirmed the status (alive or dead) of marmots with radio implants at least twice per month during the active season, except during September 2002 and May 2003, when status was checked only once per month. We found two transmitters beneath the snow outside the burrows in May 2003 – these animals were presumed to have died prior to initiating hibernation in September 2002.

We used two measures of reproductive success: weaning success and litter size. Weaning success was defined as the proportion of adult females present in late June that weaned litters (infants appearing above ground), determined by observing females and their primary burrows several times per week during mid-July through August. Litter size was determined by observing the litter on several occasions within 10 days of emergence, a period when infants remain close to the natal burrow and are easily counted. Whenever possible, we trapped and marked the infants to facilitate counting. Females at Obstruction Point and Marmot Flats in 2002 and Royal Basin in 2003, 2004, and 2005 were checked only once every 10-14 days. In some cases the mobility of infants when we discovered them suggested that they had been above ground for more than a week. We excluded these litters from the analysis of litter size because it was possible that some infants had already been lost to predation.

We determined apparent survival for each juvenile from initial tagging in the year of its birth until the following spring, when it was considered a yearling, based on whether the animal was trapped or resighted (ear-tag numbers read with binoculars or spotting scope) in May or June. In addition to intensive spring trapping and regular observation, we conducted scheduled "resighting" sessions at each site in late June, attempting to positively identify all marmots present on each of 3 days. Our estimated detection probabilities approach 1.0 over the three days, and no yearling that we failed to detect prior to 1 July was later trapped or resighted (S.C.G., M.L.T. & L.S.M., unpublished data).

Statistical Analyses

Behavioral Data

We used a multivariate analysis of variance (MANOVA; SPSS version 12.0) to examine the effect of visitation on the suite of six looking-up and flight-response behaviors. Prior to fitting the MANOVA, we used correlations and general linear models to determine whether distance to burrow influenced flight distance and whether foraging group size influenced any of the three looking-up responses. We found no significant relationships, so we did not include distance to burrow or foraging group size in the MANOVA. We used the z scores (to standardize the disparate units and scales) of the log-transformed variables as the dependent variables in the MANOVA, with level of visitation as a fixed factor. After establishing overall model significance, the effect of visitation on the individual response variables was examined.

In addition to the MANOVA, we used discriminate function analysis (DFA) to evaluate whether the marmots at the low-use demographic sites behaved similarly to

those at the low-use behavioral sites. We used a stepwise entry procedure (discriminate: method=Wilks, p to enter ≤ 0.15) to develop a function that best discriminated between marmots at the high- and low-use sites based on the looking-up and flushing data from the 13 behavioral sites.

We used the resulting classification function, built using data from the behavioral sites, to assign marmots from the low-use demographic sites to either the high- or low-use categories, based on their looking-up and flushing responses. However, we did not collect all response variables on every marmot at the demographic sites. In these cases, the mean value of the cases used to build the model was substituted for the missing value. The use of mean values rather than actual data is not ideal for DFA; it results in conservative discriminate function scores that are closer to the cut point than they might be otherwise. However, the direction of the deviation from the cut point and the resulting group classification was determined by the variables that were measured on each animal.

Finally, we conducted a second MANOVA to determine if the overall pattern of activity of marmots varied at the high- and low-use sites. We converted the time each marmot devoted to each of the five activities in the activity budget to a proportion of the total time available to that individual. To reduce heterogeneity of the variances and increase residual normality we transformed data to the arc-sine square root. Because vigilance was strongly correlated with other ($r = -0.719$, $p = 0.006$) and with below ground ($r = -0.688$, $p = 0.009$) and we were interested primarily in vigilance behavior, the other two variables were not included in the MANOVA. The remaining activities (vigilance, foraging, and traveling), together with total time (time from the marmot's first

appearance until the afternoon move to the burrow), were used as the response variables with visitation as a factor.

Demographic Data

The potential effect of human disturbance on the body mass of 117 marmots ≥ 1 year old was evaluated at high- and low-use sites in a mixed linear model. Our sample of infants was too small and unbalanced to include them in this analysis. We initially fit a model that included visitation as a fixed effect, Julian date as a covariate, and six age-sex classes (yearling, 2-year-old male, 2-year-old female, adult male, adult nonreproductive female, and reproductive female). Because we had multiple measurements per animal (range = 1-10, median = 2), we included the individual marmot as a random effect nested within site. After examining the residuals, we added an interaction term, Julian date * class, allowing for different age classes to gain weight at different rates across the summer, and a quadratic term, Julian date^2, to account for a tendency for animals to gain weight most rapidly at the beginning of the summer. Parameters were estimated with restricted maximum likelihood.

We used known-fate models in program Mark (White & Burnham 1999) to compare survival of radio-implanted marmots at high- and low-use sites (Table 2). We developed a set of a priori models for bimonthly survival during the active period (approximately 1 May– 1 October). No radio-tagged marmot died during hibernation, so we set survival during that period equal to 1. These models potentially included sex, age, and visitation as individual covariates. Because it was also biologically reasonable that pulses of mortality occurred during particular times of year (Bryant & Page 2005), some models included one parameter for September survival, applied to all marmots, that was

estimated separately from May-August survival. We also estimated a separate parameter that allowed adult female survival to differ from the rest of the population in June, a period when females are potentially under increased stress during pregnancy and lactation.

Our interest lay in testing the hypothesis that visitation reduces marmot survival, rather than estimating parameters or selecting models. Thus, we used AIC_c values to identify the most parsimonious model that included the visitation effect (Burnham & Anderson 2002) and then performed a likelihood ratio test on nested models with and without visitation to test for an effect of this parameter (Cooch & White 2006; Wolfinger 1993). This approach allowed us to identify the most likely model structure of our candidate set and obtain a significance level for the factor of interest, namely visitation, given that model structure.

Weaning success and apparent infant survival for the two visitation groups were compared with chi-square tests, and litter size was compared with a two-sample *t* test. Because reproductive and infant survival data from low-use sites were relatively sparse, we also made qualitative comparisons of rates from high-use sites with those measured for Olympic marmots during a period of relative stability (1967-1969; Barash 1973) and two other North American species for which long-term data are available (M. vancouverensis, Bryant 2005; M. flaviventris, Schwartz et al. 1998).

RESULTS

Looking-up and Flight Behavior

Marmots exhibited clear differences in looking-up and flight behavior between the visited and unvisited sites (Fig. 2). The MANOVA indicated an overall effect of visitation ($F_{31}^{6} = 3.326$, $p = 0.012$), with significant univariate differences observed in five of the six behaviors. During the 2-minute foraging bouts, marmots at high-use sites looked up more often than marmots at low-use sites ($p = 0.003$) and, ultimately, devoted a greater amount of time to looking up ($p = 0.022$). The duration of each look up was essentially the same at high- and low-use sites ($p = 0.847$). Marmots at high-use sites allowed humans to approach to a distance of less than half that tolerated by marmots at remote sites before fleeing to ($p = 0.012$) and then entering the burrow ($p = 0.030$). Once the human withdrew, the marmots at the high-use sites typically remained in their burrows less than a minute, whereas marmots at the unvisited sites took several minutes to reemerge ($p < 0.001$).

The DFA stepwise procedure identified number of looks and exit delay as the two variables most useful in discriminating between marmots at low- and high-use behavioral sites. The resulting function significantly discriminated between groups (Wilks' lambda = 0.617; $X_{2}^{2} = 16.89$; $p < 0.001$) and correctly assigned group membership to 71% of the 38 marmots used to build the model. When applied to the marmots from the low-use demographic sites, this same function assigned 70% (7 of 10) animals to the low-use category, confirming that marmots at these sites retained behavioral traits of the most naïve marmots, despite disturbance related to our trapping and telemetry work.

Activity Budget

In contrast to the differences observed in the flushing and vigilance behavior of visited and unvisited marmots, the overall pattern of marmot daily activity did not differ

as a function of visitation ($F_8^4 = 1.435$, $p = 0.307$) and visitation did not affect any of the individual activities (all $p > 0.05$; Fig. 3). However, there was a tendency for marmots at high-use sites to spend more time in miscellaneous (other) activities ($p = 0.073$). This difference arose because several marmots at high-use sites spent considerable time (in one case 72 min) in activities related to humans, such as licking roads or places where campers had urinated. Qualitatively, there did not appear to be any tendency for the timing of foraging activity to vary between low- and high-use sites as a function of the timing of tourist activity (Fig. 1). Only once during the activity budget observations did a marmot enter a burrow in response to a tourist.

Condition, Survival, and Reproduction

Current levels of tourism did not appear to affect Olympic marmot body condition or demographic rates. The mixed model analysis on 334 mass measurements from 117 marmots ≥ 1 year old indicated that tourism levels did not influence marmot body condition at our sites. The visitation parameter was not statistically significant ($p = 0.669$), and the estimated marginal difference of 0.035 kg between marmots at low- and high-visitation sites was <1% of the body mass of a breeding female and smaller than the precision of our measurements.

Out of 62 marmots with surgically implanted radio transmitters, 15 mortalities were confirmed by recovery of the radio transmitter, and 11 marmots disappeared at the same time we lost the signal. The patterns of signal losses were generally inconsistent with transmitter failure or animals moving off the study area (S.C.G., M.L.T., and L.S.M., unpublished data); it is probable that most or all of these animals were killed. However, we conducted survival analyses on two data sets. In the first, we treated 9 of

these 11 animals as having died during the period in which we first were unable to locate

the radio; removed from the data set 1 of the 11 marmots because its signal was never

heard following the surgery; and assumed that the final marmot, which carried a very old

transmitter for which a signal was lost in late September, had successfully hibernated

with a failed radio. In the second data set, we assumed that the missing transmitters had

failed or the animals had left the study area and we removed them from the data set

beginning in the time-period in which they disappeared (i.e., they were right-censored).

Regardless of the treatment of the missing marmots, visitation did not affect survival

rates. Of our candidate model set, a model that included parameters for September and

adult females in June had the most support based on AIC_c values. The likelihood-ratio

test indicated that inclusion of the visitation parameter did not significantly improve

model fit regardless of whether the missing marmots were assumed dead ($X_1^2 = 0.370$, p

$= 0.54$) or were censored ($X_1^2 = 0.85$, $p = 0.36$).

Similarly, infant survival was not depressed at any of our sites. At high-use sites,

55% (22 of 40) of tagged infants were resighted or trapped the following spring; 50% (10

of 20) of tagged infants at low-use sites were similarly identified in the spring. These

proportions are statistically indistinguishable ($X_1^2 = 0.008$; $p = 0.93$) and similar to those

measured in Olympic marmots during a period of population stability and other marmot

species (Barash 1973; A. A.Bryant personal communication; Schwartz et al. 1998).

Neither weaning success nor litter size was lower at the high-use sites than at the

low-use sites. Weaning success was determined for a total of 29 and 36 adult females at

high- and low-use sites respectively. A greater proportion of females produced litters at

the high-use sites (59%) than at low-use sites (31%, $X_1^2 = 4.08$; $p = 0.043$), a difference

largely driven by low reproduction at Royal Basin (Table 2), where a very high density of marmots may have resulted in reproductive suppression (Blumstein & Armitage 1998; Hacklander et al. 2003; Wasser & Barash 1983). Litter size was similar across visitation levels ($t = 0.615$; $p = 0.55$), averaging 3.75 at the low-use sites and 3.46 at high-use sites. Both weaning success and litter size were similar to those seen in other marmot species (Fig. 4).

Discussion

If changes in animal behavior resulting from direct human disturbance are to negatively affect the persistence of a given species or population, these changes must lead to reduced demographic performance (Gill et al. 2001). Our results indicate that Olympic marmots frequently exposed to hikers and vehicular traffic exhibit reduced sensitivity to humans, as manifested by shorter flight distances and decreased hiding time following disturbance, and that these marmots also look up more frequently while foraging. However, analysis of existing demographic data showed that these behavioral changes were not associated with decreased survival, reproduction, or body condition.

Until now, the supposition that marmots can adjust their behavior to avoid negative demographic consequences when confronted with regular human presence has been based on potentially ambiguous behavioral data (Louis & Le Berre 2000; Neuhaus & Mainini 1998). Our demographic results support this hypothesis in the case of Olympic marmots and demonstrate the importance of using demographic data when evaluating the impacts of recreational activities on animal populations.

Comparison of Behavioral and Demographic Results

If one relied on a single behavioral metric to evaluate the probable impacts of disturbance on marmots – and perhaps other species – the conclusions would depend on the behavioral trait examined. The flushing experiments revealed that Olympic marmots in areas of high tourist traffic responded to the approach of a human in much the same way as alpine marmots in highly visited tourist areas (Louis & Le Berre 2000; Mainini et al. 1993; Neuhaus & Mainini 1998), flushing only when humans approached quite close (Fig. 2). However, these data provided inconclusive information about the potential for associated demographic effects. The reduced flushing responses in marmots regularly exposed to humans could have indicated that these marmots had learned that the danger presented by a car or human is low; that regularly visited marmots were energetically stressed and therefore the cost of lost foraging opportunity was higher than for unvisited marmots; or that regularly visited marmots were less wary because they had been "desensitized" to movement, potentially leaving them vulnerable to predation.

The increased frequency with which marmots at high-use sites looked up to scan for predators when foraging further complicates the story (Fig. 2). This behavioral change was consistent with an increased wariness (perhaps because the marmots were anticipating disturbance), and may have signified a reduced susceptibility to predation. However, the resulting increase in total looking-up time potentially limited food consumption. Finally, if one compared only the amount, or temporal distribution, of time spent foraging between the two groups of marmots, one might have concluded that there was no cost associated with disturbance.

The demographic data, on the other hand, were unambiguous. Olympic marmots successfully accommodated current levels of tourism without changes in reproduction or

survival. The behavioral changes neither caused nor were symptomatic of a negative energy balance. Body mass, which influences marmot reproductive success (Hacklaender & Arnold 1999) and infant survival (Lenihan & Van Vuren 1996), was essentially unaffected by visitation level. The 100% overwinter survival of radio-tagged marmots, normal fall-to-spring apparent survival of tagged infants, and similar reproductive output at both types of sites all suggest that energy balance is similar across sites. The similarity of reproductive and infant survival rates at high-use sites to historic Olympic marmot rates from a period of population stability and to those of related species (Fig. 4) also indicate that marmots at high-use sites are not energetically stressed. Likewise, the reduced flight response of marmots at high-use sites does not appear to indicate a functional reduction in antipredator behavior, because we detected no effect of visitation level on active season survival of radio-tagged marmots.

The similarity of marmot behavior at the low-use demographic sites and the low-use behavioral sites support our low-use designations for the demographic sites. For our low-use sites, our research activities represented all or most of the animals' exposure to humans. We visited our low-use sites ≤ 25 days each summer, often briefly for telemetry checks. Marmots at high-use sites were disturbed many times each day by cars, hikers, or both (Table 1; Fig. 1), in addition to research related activities.

Olympic Marmots and Tourists: Recommendations for Management

We do not recommend changes in current visitor management for the purpose of protecting marmots from direct disturbance by humans. Marmots at our seven high-use demographic study sites experienced the highest tourist pressure of any marmots currently found in Olympic National Park, without exhibiting reductions in key

demographic rates. It is also unlikely that recently documented extinctions were directly caused by tourism because most extinct colonies would have experienced disturbance levels similar to those we studied.

However, as wildlife viewing opportunities become rarer and park visitation increases, it may be necessary to increase efforts to keep hikers on designated trails and drivers in their cars. Predictability of human behavior is important to marmots (Mainini et al. 1993) and other wildlife (Papouchis et al. 2001). Although only once during our activity budget observations did a marmot flee from a tourist, during the course of our trapping and telemetry operations we regularly saw drivers leave their cars and pursue marmots in an effort to photograph them, following them or sitting a few meters from their burrows for as long as 40 minutes. This clearly does not constitute predictable behavior. Education and enforcement efforts could be targeted to reduce this kind of direct harassment. If tourism levels grow substantially and concerns persist about marmot populations, it would be wise to reexamine marmot responses as a threshold response to disturbance is possible (Creel et al. 2002).

We also caution that our results may not apply to marmots that recolonize or are reintroduced to popular tourist areas. Alpine marmots apparently habituate to humans during the first summer of life (Neuhaus & Mainini 1998). If true for Olympic marmots, 2-year-olds emigrating or transplanted from low-use sites might be sensitive to disturbance. No marmots immigrated to a high-use site during our study, so we could not evaluate the effects of disturbance on naïve adult marmots.

Finally, we emphasize that our finding that tourism does not negatively affect demographic rates of Olympic marmots speaks only to the impact of direct disturbance.

Our results in no way preclude the possibility that tourism may indirectly influence marmots if humans are subsidizing predators or otherwise altering the ecosystem.

Conclusions

Although our results are specific to Olympic marmots, we have demonstrated the potential for confusion that can arise if one relies on behavioral studies alone to assess impacts of recreational disturbance on populations. Demographic studies designed a priori to evaluate population performance are preferable but often impractical – the costs are too high and the delays too long. However, we expect there are other taxa for which existing demographic data could be used in a post hoc analysis similar to ours. This approach allowed us to test for biologically important demographic costs to Olympic marmots without incurring additional field expenses or delays. By eliminating from further consideration one potential cause of observed marmot declines, we may have prevented unpopular and unnecessary restrictions on tourism.

Table 9. Descriptions of study sites used for behavioral observations of Olympic marmots in 2004.

Site	UTM coordinates (easting, northing)[m]	Marmots trapped?	Activity budget date	No. Marmots[n]	Tourist infrastructure	No. tourist groups[o]
High use						
Eagle Point	469116, 5309321	yes	15 July	3	road	13 cars
Bogacheil Peak	442170, 5306070	no	18 August	3	trail	6 groups
Marmot Flats	470150, 5307814	yes	30 June	5	road	13 cars
Obstruction Point	471435, 5307188	yes	20 July	7	parking lot & trailhead	8 cars
Gladys Lake	473040, 5302750	no	10 July	5	trail & campsite	4 groups
Moose Lake	473680, 5303315	no	12 July	2	trail & campsite	2 groups
Elk Mountain	473753, 5307904	no	29 July	3	trail	3 groups
Low-Use						
Heart Lake	446200, 5306981	no	20 August	6	none	0
Happy Lake	448680, 5318100	no	23 July	5	none	0
Swimming Bear Lake	446500, 5307000	no	12 July	10	none	0
Constance Pass North	486830, 5291150	no	5 August	5	none	0
Dodger Point	462000, 5302400	no	26 July	3	none	0
Swimming Hole	473230, 5305100	no	8 July	4	none	0

[m] Universal Transverse Mercator coordinates, NAD 83 datum, Zone 10
[n] Marmots age ≥ 1 year old seen at the site during the behavioral observations.
[o] Groups of hikers or tourist cars seen during the morning activity period (0700-1300 hours).

Table 10. Sites used for demographic analysis of the effects of tourism on Olympic marmots.

Site	UTM coordinates (easting, northing)	Tourist infrastructure	Years of study	No. marmots with transmitters	No. 15-day transmitter periods	Females (litters)
High use						
Eagle Point	469116, 5309321	road	2002-2005	7	107	4 (3)
Marmot Flats	470150, 5307814	road	2002-2005	13	170	11 (7)
Obstruction Point	471435, 5307188	parking lot & trailhead	2002-2005	5	96	11 (5)
Wolf Creek	461722, 5313233	trail	2002-2005	2	19	0[p] (0)
Hurricane-Elwha Junction	460352, 5315334	trail junction	2002-2003	2	7	0 (0)
Pull-Out	469523, 5308374	scenic overlook (road)	2003-2005	3	18	2 (1)
Zenith	460768, 5315211	trail end & overlook	2002-2005	1	27	1 (1)
Total high use				33	337	29(17)
Low use						
Royal Basin	483700, 5296750	none[q]	2003-2005	16	241	27 (7)
Lower Ridgely	460857, 5314961	none[r]	2002-2005	0	0	0 (0)
Pumpkin Seed Lake	471514, 5306428	abandoned trail[s]	2003-2005	7	66	4 (4)
Jon's Basin	460157, 5315559	none[t]	2002-2005	5	77	5 (0)
Total low use				28	384	36(11)

[p] Females were present at Wolf Creek in all years but were not considered because there was no male present.

[q] There is a trail in Royal Basin on the far side of the valley (>200 m) from the marmot meadow. We have only once in 3 years seen a hiker on or near the meadow itself, which is very steep and separated from the trail by a marsh.

[r] Lower Ridgely is isolated from hikers, but the female was not included in the analysis of reproductive output because she occasionally traveled to an area where she would have encountered visitors. The infants from a litter in 2004 never traveled into the tourist area and were used in the infant-survival calculations

[s] Of the low-use sites, Pumpkin Seed Lake had the most tourist pressure – we estimated that one or two groups of hikers visit this site in a typical week and on two occasions, campers were seen on our arrival in the morning (S.C.G., personal observation), although camping was banned in this area.

[t] There is a trail along the rim of Jon's Basin from which hikers sometimes look down, but we never saw a hiker descend into the basin, which is extremely steep and rocky.

Figures

Figure 1. Average time (minutes) that hikers and vehicles were visible to focal Olympic marmots at seven sites with high tourist levels (high use) during each hour of morning observation periods, and the average time spent foraging by focal marmots at seven high-use sites and six low-use sites. No tourists were seen at the low-use sites during the morning observation periods.

Figure 2. Medians (solid horizontal line), 25th and 75th percentiles (bottom and top respectively of shaded area), 10th and 90th percentiles (bottom and top whiskers respectively), and outliers (circles) of the untransformed behavioral observations collected on Olympic marmots at sites with high levels of tourists use ($n = 18$ marmots) and low levels of tourist use ($n = 20$). Data shown are for (a) number of times a marmot looked up per minute during the 2-minute observation period, (b) average duration of each look, (c) total time spent looking up per minute, (d) distance at which marmots fled to their burrow in response to an approaching human, (e) distance between an approaching human and marmots that prompted marmots to enter their burrows , and (f) time the marmots remained in their burrows after the human withdrew.

Figure 3. Time devoted by Olympic marmots from low-use and high-use tourist sites to each of six behaviors (described in the text) during the course of the morning on which the marmots were observed.

Figure 4. Mean reproductive rates and infant apparent survival rates (weaning to spring) of contemporary Olympic marmots at sites with high and low levels of tourism (this study), Olympic marmots in the 1960s (Barash 1973), Vancouver Island marmots (weaning success and litter size, Bryant 2005; infant survival, A. Bryant, personal communication), and yellow-bellied marmots in Colorado (Schwartz et al. 1998). Error bars represent 95% confidence intervals for the means. Sample sizes are shown in the base of the bars.
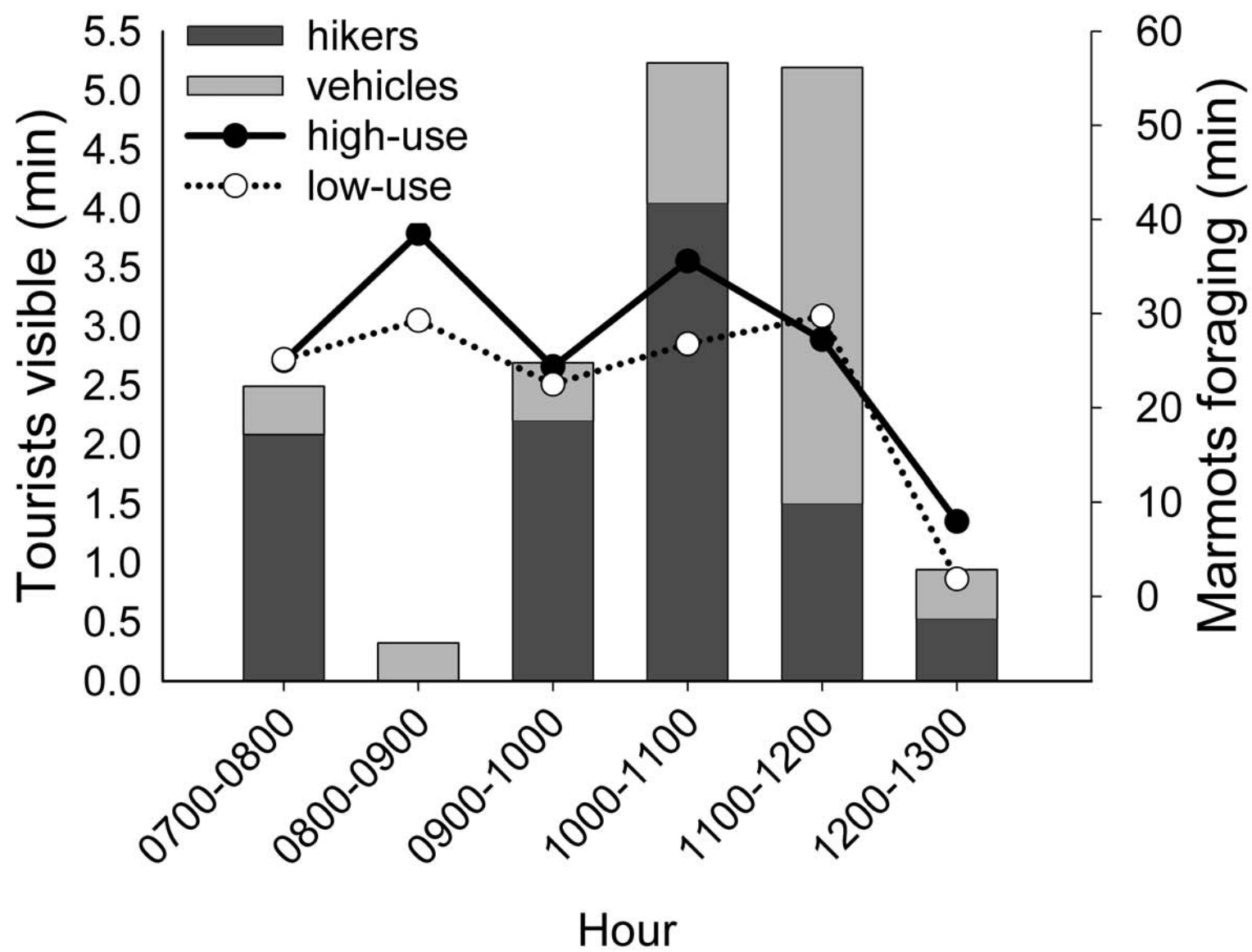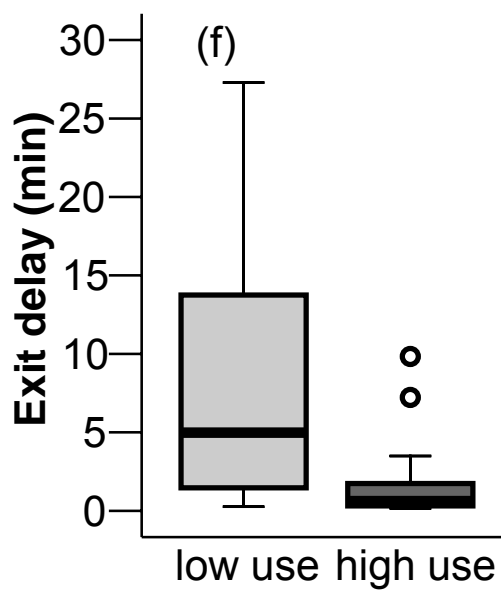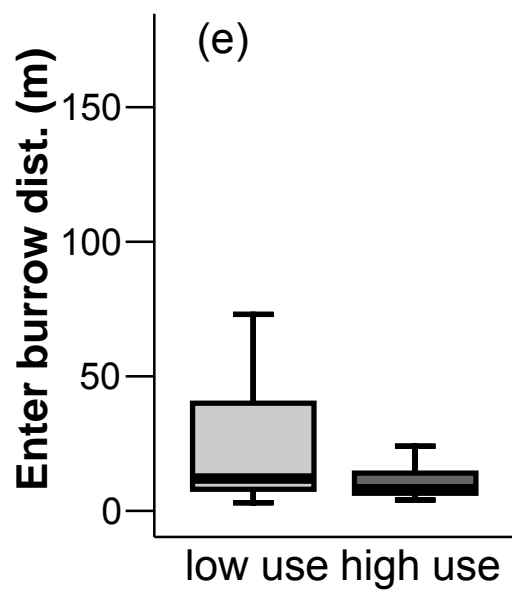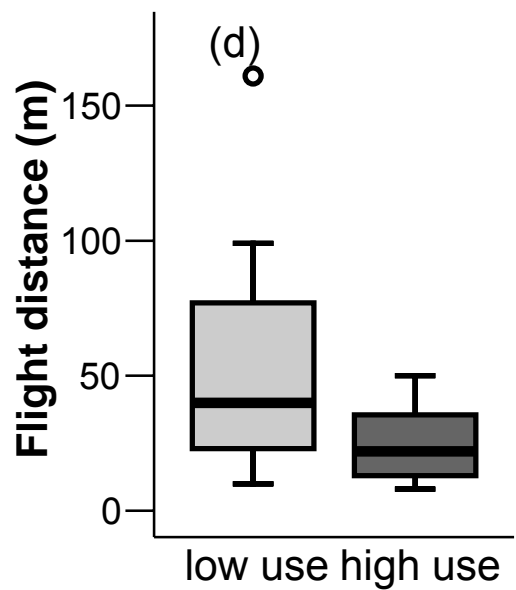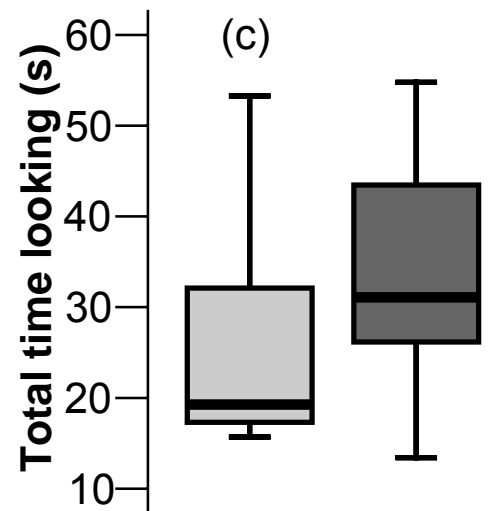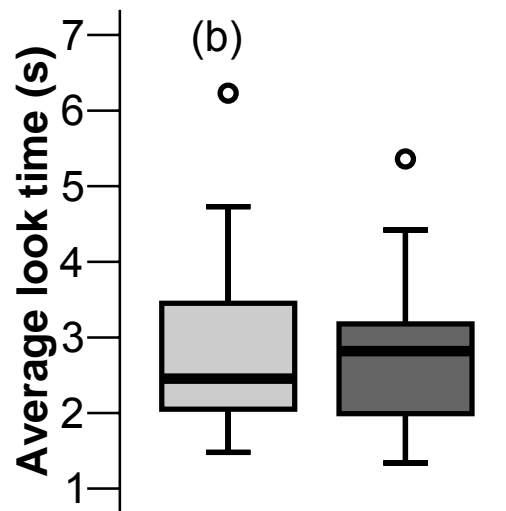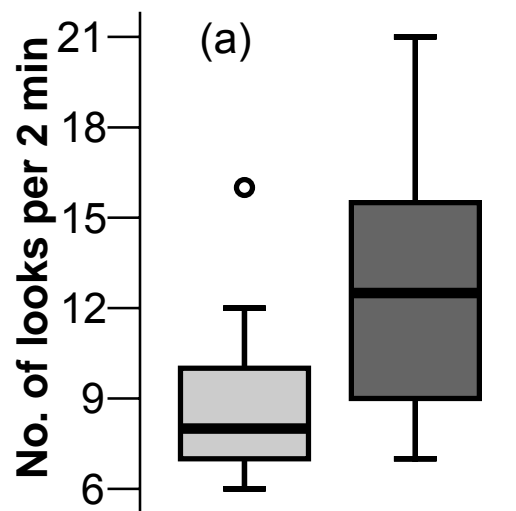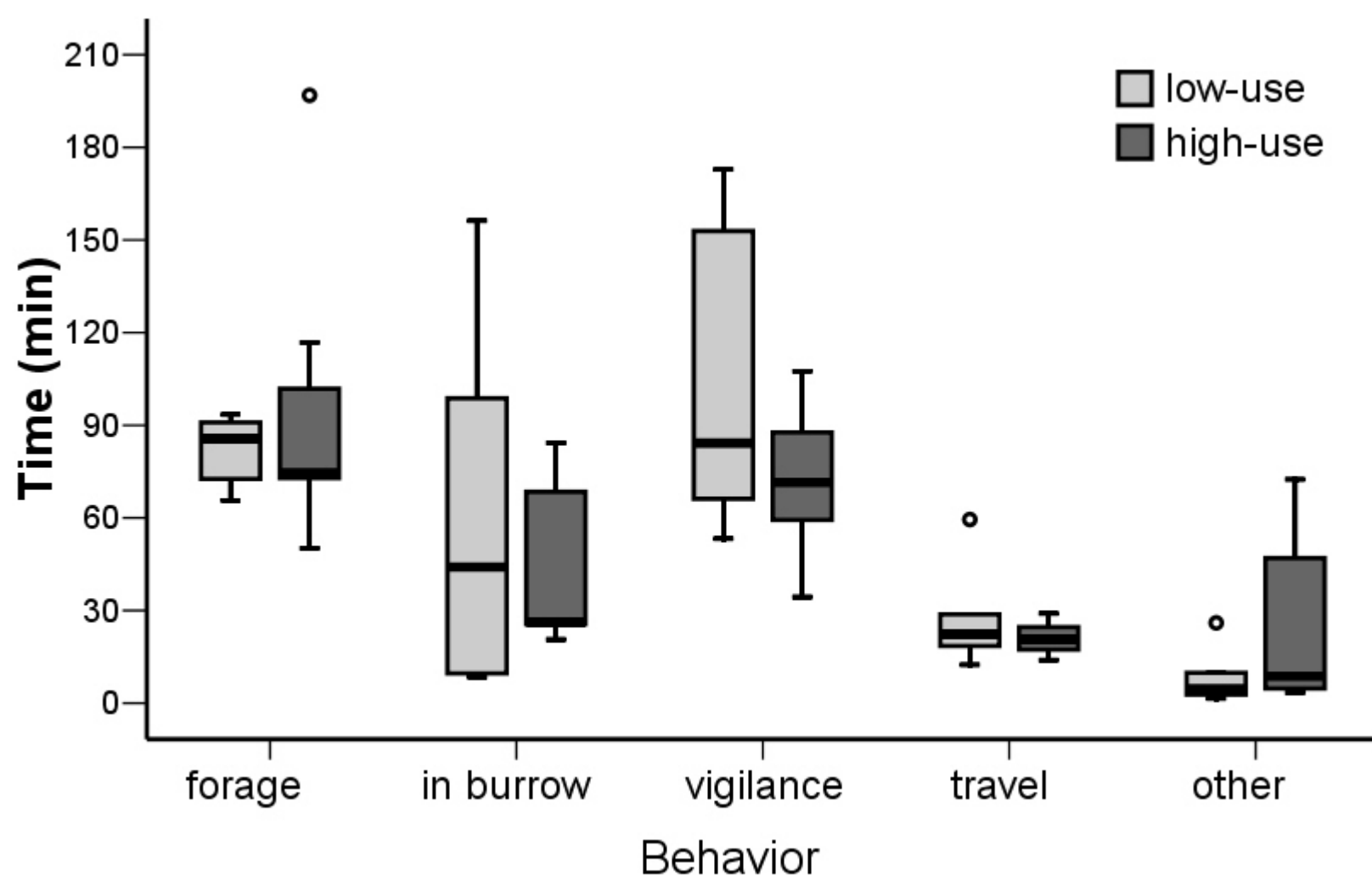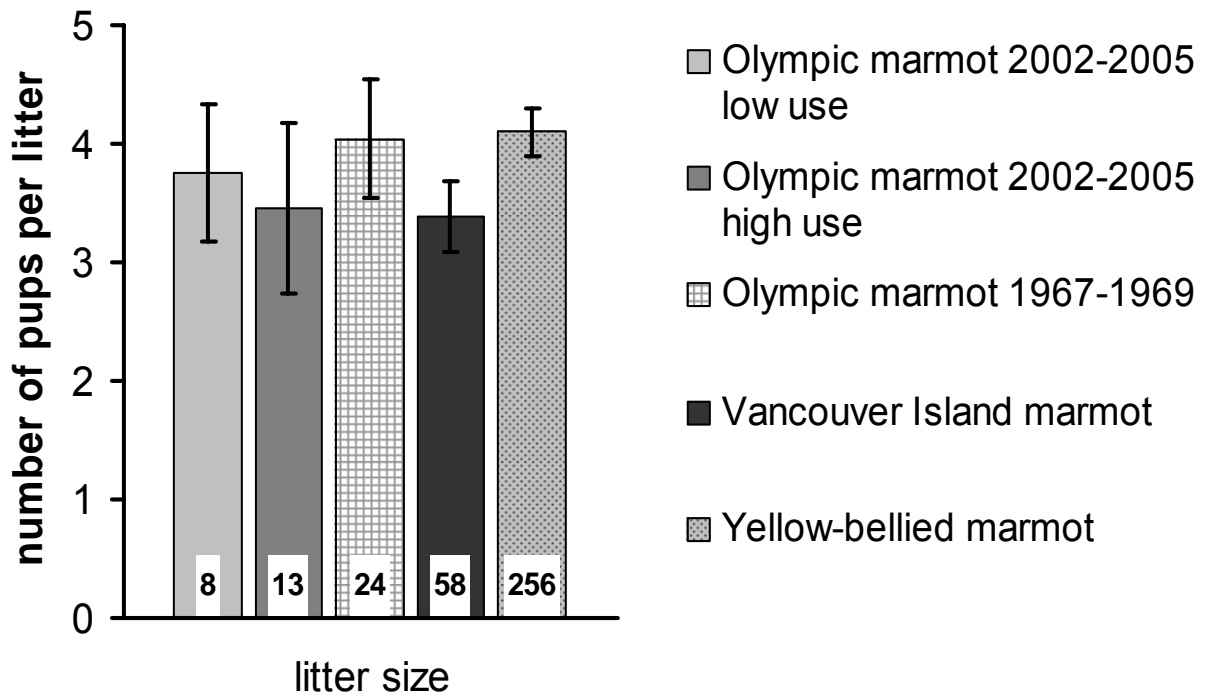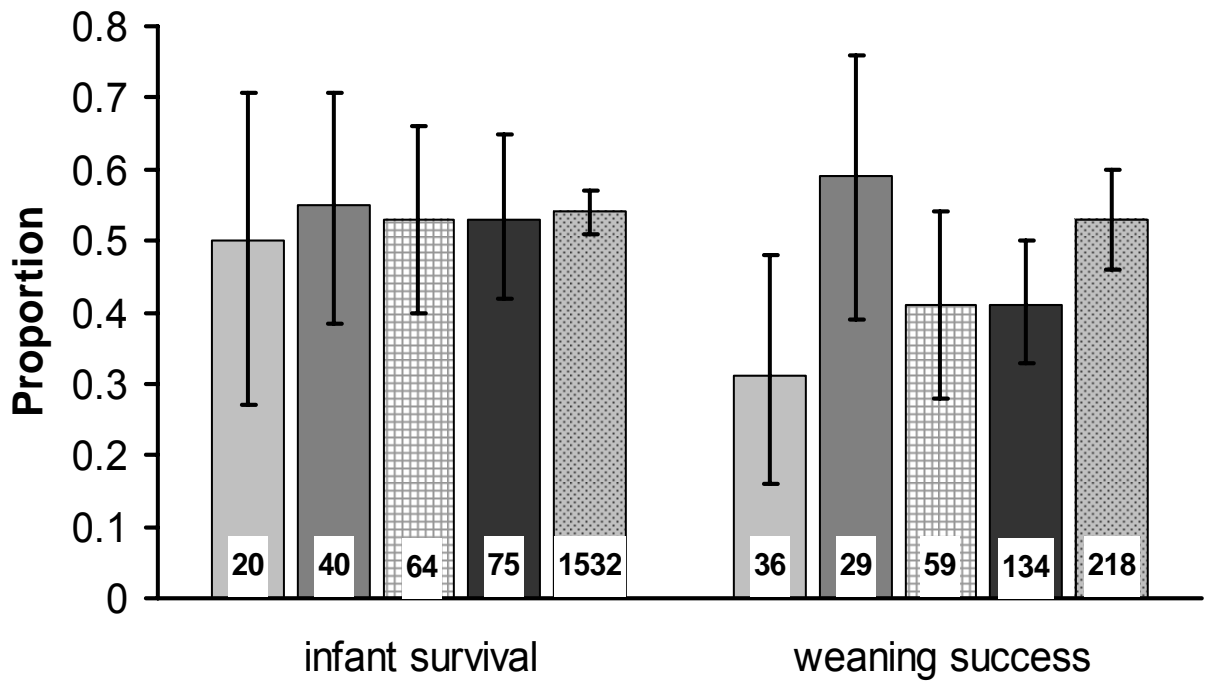
CHAPTER 3.

FEMALE OLYMPIC MARMOTS (*MARMOTA OLYMPUS*) REPRODUCE IN CONSECUTIVE YEARS

Abstract.– Olympic marmots (*Marmota olympus*) are reported to skip at least one year between reproductive efforts. We observed several female marmots weaning infants in consecutive years. There was no evidence that reproductive skipping was more common than annual reproduction. High spring food availability resulting from climate change may allow females to wean consecutive litters regularly.

INTRODUCTION

Life-history traits such as age of first reproduction, litter size, frequency of reproduction, and survival often vary across and within species as a function of environmental conditions or local density (Arendt & Reznick 2005; Dobson & Murie 1987; Oli et al. 2001; Reznick & Endler 1982). Changes in life-history parameters can have significant impacts on population growth rate (Oli & Dobson 2003), so the degree of plasticity in these parameters may dictate whether a species can successfully survive environmental change or other stressors, or respond favorably to habitat enhancement by management.

Olympic marmots (*Marmota olympus*) are large ground-dwelling squirrels endemic to the mountains of the Olympic Peninsula, WA, USA. Like other high-elevation marmots, they hibernate for 7-8 months a year, with snow cover preventing

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foraging from September through May or June. This leaves a narrow window available for growth, reproduction, and accumulation of fat necessary for hibernation. Olympic marmots, and the closely related hoary (*M. caligata*) and Vancouver Island marmots (*M. vancouverensis*), delay any dispersal until after the second hibernation, first reproduce at age three or four, and breed infrequently thereafter (Barash 1973, 1974; Bryant 2005). Female hoary and Olympic marmots are reported to not wean litters in consecutive years (Barash 1973; Holmes 1984; Wasser & Barash 1983); Vancouver Island marmots seldom breed in consecutive years in the wild (Bryant 2005). Females should be under selective pressure to produce as many successful offspring as possible so there must be a compelling reason for them to forego annual reproduction.

The proximate causes of reproductive skipping in female alpine-dwelling marmots are not fully resolved. The immediate costs of reproduction appear to be particularly high in these species. Reproductive females typically do not begin mass gain until after lactation ends in late-July, and so, in just 6-8 weeks must accumulate enough fat to survive hibernation. Reproductive females forage more at dawn and dusk (Barash 1980) and remain active later in the fall than their non-reproductive counterparts (Barash 1976), possibly exposing themselves to an increased risk of predation (S. C. Griffin, pers. obs.). Despite the additional time spent foraging, reproductive females enter hibernation at a lower body mass (Barash 1989b) and may risk over-winter mortality (Armitage et al. 1976). There is evidence that reproductive success in other *Marmota* species is dependent on spring body condition (Hackländer & Arnold 1999) and duration of snow cover (Schwartz & Armitage 2005; Van Vuren & Armitage 1991), suggesting that regularly

lost reproductive opportunities are a cost of living in a harsh environment (Armitage & Blumstein 2002).

Alternatively, there is some evidence that social pressures limit reproductive effort in marmots when dominant females suppress reproduction by subdominants or delay the age of first reproduction of young animals (Blumstein & Armitage 1999; Hackländer et al. 2003). In the alpine marmot (*M. marmota*), aggressive behavior of the dominant female induces stress related hormonal changes in subdominants that prevent subdominants from successfully reproducing (Hackländer et al. 2003). When older females are present, the age of first reproduction is delayed in yellow-bellied marmots (Armitage 2007). It has been proposed that in Olympic, hoary, and Vancouver Island marmots, suppression leads to reproductive skipping (Wasser & Barash 1983).

In 2002, we began demographic studies of Olympic marmots. In this note, we report on observations of annual reproduction (i.e. successful weaning of litters in two consecutive years) by several Olympic marmots during the first four years of our study, and consider the evidence these data provide for environmental harshness and reproductive suppression as driving mechanisms of reproductive skipping.

OBSERVATIONS

As part of an ongoing study, Olympic marmots from 14 colonies located on Hurricane Ridge, Obstruction Point, and in Royal Basin (elevation 1500 – 1800 m) in Olympic National Park have been monitored since 2002 or 2003. All marmots were marked with uniquely numbered ear-tags and a subset implanted with radio-transmitters.

Adult female marmots and their primary burrows were observed multiple times each week mid-July through August to determine which females successfully weaned litters. When we found a litter, we attempted to trap and mark the infants within a week of discovery to facilitate counting them. Alternatively, we observed the infants on several occasions during the first 10 days following emergence to determine litter size. Infants remain close to their natal burrow and so are easily located and counted during this period. We began observations at most colonies in 2002. Therefore, 2003 was the first year in which it was possible to observe annual reproduction. We began studying marmots at two sites in 2003, and so could not have observed annual reproduction at these sites until 2004. We refer to the first of the two litters weaned by the same female in consecutive years as the "first" litter and the second of these litters as the "second" litter.

Reproduction in consecutive years by Olympic marmot females was relatively common during our study (Table 1). Several females produced second litters in 2004 and 2005, and one female weaned three successive litters. Of 17 females that produced litters in one year and survived to the following July, seven (41%) successfully weaned a second litter. Of 29 marmots that skipped the previous year despite being of breeding age, 13 (45%) produced litters. Of the remaining population of 37 three-year-olds and animals whose success in the previous year was unknown 14 (37%) produced litters. The proportions of reproducing females in these three groups are not statistically different ($\chi_2^2 = 0.44, P = 0.8$). During this time, 14 adult females were present for ≥ 3 years. Only three of these (21%) demonstrated the stereotypical "reproductive skipping" by producing two litters with a single year between, while five (36%) failed to reproduce in ≥ 2 consecutive years .

Breeding in consecutive years did not result in lower reproductive output in the second year, as might be expected if females were energetically stressed (Table 2). The number of infants in the seven second litters (3.29 ± 0.95; mean $\pm$ SD) was the same as in the first litters produced by the same females (3.29 ± 1.11; [for the female that produced three consecutive litters, the 2004 litter was included twice: once as a second litter paired with the 2003 litter and once as a first litter paired with the 2005 litter]). In all cases, related yearlings and infants appeared to mix freely.

Females produced second litters under conditions of intermediate densities and in a range of social situations (Table 2). No female at Royal Basin, the largest, most densely populated site (> 5 marmots ha^{-1}; S. C. Griffin, pers. obs), produced litters in consecutive years. Although 7-10 adult females were present each year at Royal Basin, reproduction was generally low – only three females successfully weaned a litter and then survived to the following summer. Likewise, no female bred in consecutive years at any site where densities of marmots were extremely low (< 1 marmot ha^{-1}).

All second litters occurred in 2004 and 2005, years of early spring melt-out (Table 1). No second litters occurred in 2003 when snowpack was approximately normal, although the sample size was small, with only three females alive that year known to have littered in 2002.

<center>DISCUSSION</center>

During the years 2003-2005, no evidence exists that skipping was the predominant reproductive pattern in female Olympic marmots. Our data are too

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preliminary to conclude that annual reproduction is common in Olympic marmots but it could be under certain conditions. Our observations are consistent with the hypothesis that environmental harshness leads to reproductive skipping in high-elevation marmots (Armitage & Blumstein 2002) and, importantly, suggest a potentially positive response to climate change for this species.

In particular, the availability of early spring forage may dictate whether high-elevation marmots can breed in consecutive years. Hoary marmots, high-elevation (3400 m) yellow-bellied marmots, and (until this study) Olympic marmots have all been reported to skip one or more years between weaning litters (Barash 1973; Holmes 1984; Johns & Armitage 1979; Wasser & Barash 1983). However, Johns and Armitage (1979; fig. 1) indicate that snow covered the majority of their study area well into June in all years, and Barash (1973; Wasser and Barash, 1984) studied both Olympic (Table 1) and hoary marmots during periods of generally higher spring snow packs (Mote et al., 2005). All observed second litters in this study occurred in the two years of early spring melt-out (Table 1). Mid-elevation (2900 m) female yellow-bellied marmots (which often breed annually) have higher reproductive success in years with earlier snowmelt (Schwartz & Armitage 2005; Van Vuren & Armitage 1991). Thus, when food resources are scant in May, females of many high-elevation *Marmota* may be forced to skip a year to recoup body condition, whereas in years of abundant spring forage, they are capable of breeding in consecutive years. If this is true, consecutive year reproduction will become more common if spring snow-pack continues to decline in the Olympic Mountains.

Our observations provide less support for a release from high population densities as a cause of consecutive year reproduction. Although we did not observe annual

reproduction at the most densely populated site, females did reproduce in consecutive years at several sites where marmot densities were similar to those recorded by Barash (1973). Similarly, our limited data do not directly support the reproductive suppression hypotheses, although we cannot rule out the possibility that reproductive suppression may occur in particular situations (Armitage 2007). To effectively evaluate this would require substantial behavioral, demographic, and, optimally, hormonal data to evaluate the influence of older or dominant females on the stress levels and reproductive success of subdominant or younger animals (Hackländer et al. 2003).

There has been considerable concern about the potential impacts of climate change and increased predation on high-elevation species, including marmots (Bryant & Page 2005; Inouye et al. 2000; Krajick 2004), and both Vancouver Island marmots and Olympic marmots have declined in the last two decades (Bryant 1998). Annual reproduction potentially represents a positive response to a warming climate or reduced densities resulting from predation, but it represents only one piece of the story. Recovering and protecting these species in the face of simultaneous changes in predation pressure, climate, and other yet to be identified factors will require an understanding of how marmot reproductive, survival, and dispersal rates respond to changing densities and resource availability. Future studies should include a component directed at partitioning the relative importance of conspecific densities, local social structure, individual body condition, habitat and weather in determining whether an individual breeds annually or skips one or more years.

Table 1. Frequency of annual breeding in Olympic marmots (*Marmota olympus*; *n* represents the number of females available to wean second litters) and corresponding May 1 snowpack at Cox Valley, Olympic National Park, Washington, USA as a percent of the 1968-2005 average. The Cox Valley snow course is located on a north-facing slope of Hurricane Ridge at 4750'.

Year	Snowpack May 1[21]	Females weaning second litter
1968	98%	0% (*n=5*)[22]
1969	147%	0% (*n=3*)
2003	86%	0% (*n=3*)
2004	68%	57% (*n=7*)
2005	14%	43% (*n=7*)

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[21] Snowpack data are from the USDA Natural Resource Conservation Service, National Water and Climate Center and can be accessed online at http://www.wcc.nrcs.usda.gov/snowcourse/sc-data.html
[22] 1968 and 1969 reproductive data from (Barash 1973)

Table 2. Summary of reproductive efforts and social environment of Olympic marmots (*Marmota olympus*) that successfully weaned litters in consecutive years. Shown are the year of the first and second litter with litter size in parentheses, and the number of females in social group in year of second litter. One female weaned litters in three consecutive years – she is represented twice in the table.

Female	1st litter year (size)	2nd litter year (size)	Females in social group
Miwa	2003 (2)	2004 (3)	1[23]
Beanbag	2003 (3)	2004 (3)	2[24]
Nao	2004 (4)	2005 (4)	1
Graygirl	2003 (2)	2004 (2)	1[25]
Matt's Marmot	2004 (5)	2005 (3)	1
Lena	2003 (3)	2004 (5)	2[26]
Lena	2004 (5)	2005 (3)	1
Litter size $\pm$ SD	3.29 $\pm$ 1.11	3.29 $\pm$ 0.95	

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[23] Home range abutted another adult female that produced litter of 6 infants.
[24] Subordinate produced litter of 6 infants
[25] Home range abutted a non-reproductive adult female
[26] Subordinate produced litter of 4 infants

CHAPTER 4.

PREDATION BY A NON-NATIVE VERTEBRATE DRIVES DECLINE OF AN

ENDEMIC MAMMAL IN A NATIONAL PARK.

INTRODUCTION

Historically, the prevention of habitat destruction and harvest within national parks and other protected areas has been adequate to protect many species from catastrophic decline. However, climate change, invasive species, and disease pay no heed to borders and many protected areas now experience tremendous tourist pressure. Thus, for many species, simply protecting habitat is no longer sufficient. This appears to be the case for the Olympic marmot (*Marmota olympus*), which, despite the near total inclusion of its range within the nation's fourth largest national park, has suffered recent declines (Griffin et al. in review).

Olympic marmots have declined across much of their range during the last few decades, and these declines have been continuing through 2002-2006 (Griffin et al. in review). In fact, both abundance trends and population projections based on averaged survival and reproductive rates suggest that the annual rate of decline is about 9% per year (Griffin et al. in review). This is of particular concern given the precedent of the closely related Vancouver Island marmot (*Marmota vancouverensis*), which declined to only a few dozen animals and currently persists only as a result of a successful captive breeding program.

Although virtually all the Olympic marmot's habitat is protected within Olympic National Park, major ecosystem changes have occurred, and continue to occur. These

changes suggest several possible causes of the declines. First, recreational use of the park has grown considerably in the last few decades with the high-country, where marmots occur, representing a major attraction. High levels of recreation are thought to negatively impact many species (e.g., Klein et al. 1996; Müllner et al. 2004) and are associated with changes in Olympic marmot behavior (Griffin et al. 2007b). However, birth and death rates of Olympic marmots are indistinguishable at remote and heavily visited colonies (Griffin et al. 2007b), and marmots have disappeared from many remote locations seldom visited by tourists (Griffin et al. in review). Thus tourists do not appear to be responsible for observed declines.

A second concern has been climate change, specifically higher winter temperatures and dramatically reduced snowpacks (USDA Natural Resource Conservation Service 2006). Concerns about climate change's effects on alpine species are widespread (Inouye et al. 2000; Krajick 2004), and numerous studies have found correlations between snow depth or duration and overwinter survival, particularly of juveniles (young-of-the-year) or between snowpack duration and subsequent reproductive success (e.g., Barash 1989b; Griffin et al. 2007a; Grimm et al. 2003; Van Vuren & Armitage 1991). However, Olympic marmot reproductive and juvenile survival rates are comparable to those reported in the 1960's, before the decline began, and to those reported for similar species (Griffin et al. in review; Griffin et al. 2007b), and no radio-tagged Olympic marmot has died during hibernation during five winters of widely varying severity. Therefore, the current climate conditions do not appear to be directly affecting these marmots.

Instead, evidence suggests that increased predation on females of reproductive-age (≥ 3 years) has been a key force in the decline. From 2002-2006, the average annual survival of radio-implanted members of this critical age and sex class has been just 0.69 (95% CI: 0.58, 0.78; Griffin et al. in review). This compares to a survival rate of 89% for tagged adult females during the 1960's (from Barash 1973) and is lower than has been reported for any other high-elevation marmot. Further, all of this mortality occurred during the active season. The Olympic marmot evolved in an ecosystem with few mammalian predators: wolverine (*Gulo gulo*), grizzly bear (*Ursus horribilis*), badger (*Taxidea taxus*), lynx (*Lynx canadensis*), red fox (*Vulpes vulpes*), and coyote (*Canis latrans*) were not historically present on the peninsula (Houston et al. 1994a; Sheffer 1995). Wolves were present until the early 20th century, but although wolves will prey on marmots (Bryant & Page 2005), they are primarily below-treeline ungulate specialists. Coyotes first appeared on the Olympic Peninsula at about the same time wolves were extirpated (Sheffer 1995). Coyotes are known to prey heavily on other marmot species (e.g., Parker 1986; Samson & Crete 1997; Van Vuren 1991). Because Olympic marmots evolved with relatively low predation levels, their life-history patterns may predispose the species to declines or extinctions in the presence of an effective mammalian predator.

In this chapter, I assess whether predation on adult females in general, and by coyotes in particular, could account for the continuing declines at the demographic study sites. I first determined the proportion of mortality of radio-tagged marmots that was definitively or plausibly due to coyote predations. I then evaluated the effect that changes in adult female survival rates might have on Olympic marmot population growth rates using the deterministic matrix model described in Griffin et al. (in review).

STUDY SPECIES AND STUDY AREA

The Olympic marmot is a large, social, ground-dwelling squirrel endemic to the high-elevation meadows (>1400 m) on the Olympic Peninsula in Washington State. Although closely related to the hoary (*M. caligata*) and Vancouver Island marmot (*M. vancouversensis*), the Olympic marmot has been isolated from these species for 10's to 100's of thousands of years and is genetically and morphologically distinct (Hoffmann et al. 1979; Rausch & Rausch 1971). Small groups of 3-20 marmots dig extensive burrow systems in alpine and subalpine meadows that range in size from < 5 ha to > 100 ha and are embedded in a matrix of forest, rock, and snow. Olympic marmots hibernate for 6-8 months a year, delay any dispersal until after the second hibernation, and only attain reproductive maturity at age three or four (Barash 1973). On average, <40% of reproductive age females breed in any year. Litter size is typically three or four and mortality for juveniles approaches 50% (Barash 1973; Griffin et al. in review; Griffin et al. 2007a).

Much of the Olympic Peninsula, including most of the higher elevations, is protected within Olympic National Park. The peninsula is surrounded by water on three sides and extensive lowland forest on the fourth – as a result, there are numerous endemic plant and animal species and subspecies on the peninsula, and the mammalian fauna in particular is impoverished relative to the mainland (Houston et al. 1994a). Historically present mammalian predators that have been reported to prey on Olympic or other marmots include wolves, cougars (*Felis concolor*), black bears (*Ursus americanus*), bobcat (*Lynx rufus*)*,* and American marten (*Martes Americana*) (Barash 1973; Bryant &

Page 2005; Van Vuren 2001; Witczuk 2007). In addition to the mammalian predators, golden eagles (*Aquila chrysaetos*) and numerous smaller raptors are seasonally present in the Olympic high-country. Of these, only golden eagles are known to prey regularly on adult marmots (Bryant & Page 2005; Van Vuren 2001), although it is possible that smaller raptors might take an occasional juvenile marmot.

MATERIALS AND METHODS

Identification of cause of death

From 2002-2006, 101 Olympic marmots at three groups of study sites were surgically implanted with radio-transmitters (Griffin et al. in review; Griffin et al. 2007b). Over 50% of non-juvenile marmots at the study sites received implants at some point in their lives. With the exception of about 25 transmitters, most of which were implanted in 2002, the radio-signal pulse rate was temperature sensitive and so allowed telemetric determination of the animal's status (alive or dead). The status of all animals was determined ≥ two times per month during the active season (May – September) and usually ≥ two times per week. The 101 marmots were monitored for an average of 14.9 0.5-month active season periods (range 1-47). Adult females (>=3 years; N=40) were monitored an average of 10.2 0.5-month periods (range 1-31) and adult males (N=26) an average of 16.6 periods (range 1-40). Subadults (N=56) were monitored for fewer periods on ($\bar{x}$ = 8.3; range 1-16) because they graduated to the adult classes. One hundred twenty-five hibernation events were observed for 61 marmots.

When a marmot was determined to be dead, the carcass was located as soon as possible, often on the same day. The transmitter and any substantial remains were

collected, along with other evidence, such as feathers or carnivore faeces in the area. Photos were taken, details about the site recorded (i.e., carcass buried or covered, under trees or in the open; if under trees, how big were the trees), and the location recorded with a handheld GPS unit. If there were tooth imprints in the wax coating of the transmitter, these were later identified by comparison with the skulls of potential predators. In three cases, cause of death was determined by experienced wildlife veterinarians. All substantial remains were transferred to the Burke Museum at the University of Washington, Seattle. Cause of death was assigned as coyote, cougar, raptor (usually golden eagle), unknown below ground (and not recovered), unknown terrestrial carnivore, and unknown predator. Because no carcass was ever found in a condition that led me to suspect that the animal had died for reasons other than predation, no marmot was ever observed to be acting sick, and no trapped marmot was determined to be ill by myself or the veterinarian who performed the surgeries, I assumed that all marmots that died above ground were depredated, rather than scavenged.

I took the observed proportion of mortalities caused by coyotes in the radio-tagged population to be the point estimate of the proportion of all deaths and disappearances of marmots among marmots at the study sites and applied a finite population correction to the variance (Berry & Lindgren 1996) in determining the confidence intervals around that estimate.

Population projections

To determine how reducing coyote predation might impact marmot population growth at my study sites, I decreased mortality (i.e., increased survival) of adult and

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subadult (1 and 2 year-old) marmots in a deterministic female-based matrix model for Olympic marmots (Griffin et al. in review). The model was parameterized with birth and death rates observed in 2002-2006 for each of three groups of study colonies (Western site group, Central site group, and Royal Basin) and an average for all study colonies. Thus, the survival rate for adult females (S_{af}) became $S_{af\text{-}adjusted}$ as follows:

$$S_{af\text{-}adjusted} = S_{sf} + m(1 - S_{af}),$$

where m represents the proportional reduction in mortality. The survival rate for subadults was simultaneously adjusted in the same manner. For all sites, the unadjusted model projected a declining population given the observed demographic rates (Figure 1), a result consistent with observed population trends at the same colonies. I made no adjustments to reproductive rates or juvenile survival as these rates remain unchanged from the 1960's and are comparable to those seen in similar species of marmot (Griffin et al. in review; Griffin et al. 2007b). Furthermore, I have no indication that coyotes prey heavily on juveniles. Juveniles were not radio-tagged, so I do not know the cause of mortality for the vast majority, but anecdotally, the only three juveniles for whom a cause of death was established appear to have been killed by raptors.

The population growth projections of primary interest were those occurring when 1) when m was set to the percentage of observed mortalities that were known to be due to coyote predation; 2) when $S_{af\text{-}adjusted}$ reached 0.89, the adult female survival rate observed in the 1960's (Barash 1973); and 3) when m was set to the maximum plausible percentage of mortalities that would have been due to coyote predation if coyotes were killed all the dead animals for whom a cause of predation was not definitively established. I did this for each of the three site groups and the population average.

RESULTS

Cause of death

During the course of the study, 32 radio-tagged marmots were confirmed to be dead and the signal from an additional 11 transmitter signals disappeared along with the animal (Griffin et al. in review). Coyotes appeared to be the most common predators (Figure 2; Appendix E), killing 12 of the 17 radio-tagged marmots for which a cause of death was determined to species with high confidence. Twelve deaths could only be assigned to unspecified predator ($n = 5$) or unspecified terrestrial carnivore ($n = 7$). It is probable that some or all of these were due to coyote predation. Four completely intact carcasses were recovered – three of these had been cached by coyotes and in the fourth case, a marmot had apparently survived an eagle attack and subsequently died of its wounds just inside the entrance of its burrow. Three additional marmots died in their burrows and were not recovered. During this period, a total 100 non-juveniles, with or without radios, at the study sites died or disappeared. Thus, the sample of radio-tagged dead and missing marmots represented almost 50% of the "population" of deaths and disappearances.

I assumed that the 11 missing marmots were in fact dead, rather than assuming that they were alive off the study area beyond transmitter range or alive on the study area but undetected because of transmitter failure. Multiple lines of evidence support this assumption. If the transmitters had failed and the animals remained alive on the study site, I should have relocated most animals. The 11 missing marmots were not particularly cryptic – they were trapped an average of 1.5 times each and seen in 61% of possible

resighting sessions (see Griffin et al. in review for further explanation) in the year prior to their disappearance. Further, unexpected transmitter failures were rare. Of four transmitters known to have failed, three had exceeded their expected battery life, while the median duration of the 11 missing transmitters was less than half their expected battery life and only two were at or near the end of their expected life. On the other hand, if the missing animals had dispersed off the study area, their age and sex distribution should be similar to that of known dispersers. During the study eight adult females, two adult males, and one subadult disappeared, two adult females, five adult males, and four subadults were known have dispersed off their home-ranges (Griffin et al. unpublished data), and 12 adult females, 12 adult males, and eight subadults were confirmed dead. Statistically, there was no difference between the age and sex distributions of the missing and known dead animals ($X^2 = 4.11$, $P < 0.30$), while these distributions did differ between the missing marmots and those known to have dispersed ($X^2 = 6.69$, $P < 0.04$). Furthermore, the two adult females that did disperse each moved < 300 m. We were not able to locate any missing animals from fixed-wing aerial telemetry flights. Finally, we recovered transmitters that, although still operable, had been partially crushed by coyote bites, suggesting that predators had a bite force sufficient to incapacitate transmitters by direct impact or by breaching waterproof integrity. Given all this evidence, we treated missing marmots as having died in the interval in which they were first missing.

Additional circumstantial evidence also suggests that coyote were responsible for more than the 28% of marmot deaths I attributed to them. During my study park staff and visitors reported observing six successful coyote attacks on marmots (including two on radio-tagged individuals) but only one successful attack by an eagle, despite the fact

that an aerial attack by a large raptor – and successful departure with a captured marmot – should be more noticeable than the stealthy approach used by coyotes . Furthermore, an associated study of coyote diet found >45 coyote scats containing marmot remains in the vicinity of the Central sites and an adjacent valley during 2005 and 2006 (Witczuk 2007). Because this area probably contains <75 marmots, this represents a considerable proportion of the population. The same study, which analyzed carnivore scats collected along and near high-elevation trails, determined that 85% of scats containing marmot remains were coyote scats.

Thus, at least 28% of the 43 confirmed and presumed mortalities were attributable to coyote predation. The upper and lower 95% confidence limits for this minimum proportion of the mortalities at the study site due to coyote predations were 18% and 38% respectively. The true proportion of the radio-tagged deaths for which coyotes were responsible was probably much greater: only 12% of the 43 mortalities could be attributed to other sources with confidence (Figure 2), so much as 88% of total marmot mortalities may have been due to coyotes. The confidence limits for the study sites were 81% and 96%.

Matrix model

Given the birth and death rates observed between 2002-2006, marmot populations at all three site groups were projected to decline (Figure 1, Griffin et al. in review). However, even moderate reductions in mortality resulted in greatly increased population growth rates. Reducing predation by 28% (in effect removing only the estimate of definite coyote predation) resulted in a positive projected growth rate for the Central site

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group, Royal Basin, and the population as a whole; all marmot population matrices showed positive growth with a 35% decrease in predation mortality. When mortality rates were decreased sufficiently to result in an adult female survival rate of 0.89 (i.e., a 45% - 70% decrease in mortality depending on the site group) as reported by Barash (1973), the projected annual population growth rates ranged from 8% - 19%. Finally, when mortality rates were decreased by 88% (approximately the estimated maximum possible for which coyotes could be responsible) population growth rates exceeded 17% in all cases. For each scenario, adjusting the mortality rates to the upper and lower ends of the confidence limits increased or decreased λ by 0.02- 0.04 in each case.

DISCUSSION

Successful conservation of declining species depends on detecting the decline in time to reverse it (Staples et al. 2005), correctly identifying the most important proximate causes of the decline (Caughley & Gunn 1996), and, finally, acting to eliminate or mitigate the problem. For declining Olympic marmots, obvious proximate stressors included climate change and tourism, neither of which appear harmful at current levels (Griffin et al. 2007b). However unusually low survival rates of adult females and the presence of a non-native, generalist predator suggested that predation might be driving the declines. Here, I used survival data from radio-tagged animals to evaluate whether high levels of predation by coyotes could cause populations of the relatively naïve Olympic marmot to decline. These data show that coyotes are the most common predators on marmots at my study sites and that even modest predator mortality is likely to cause marmot population growth rates to decline substantially, indicating that the

current level of coyote predation is a significant stressor on intensively monitored Olympic marmot populations.

It is impossible to say with certainty that coyotes are responsible for local declines or extirpations in other portions of the range as data from radio-tagged animals were restricted to colonies comprising < 10% of the species distribution. However, DNA and diet analyses of carnivore scat indicate that coyotes are present throughout the Olympic National Park high-country and that marmots constitute >10% of the coyote summer diet in several other areas where the two species are sympatric (Witczuk 2007). Given that marmots have disappeared or occur at unusually low densities in many areas of their range (Griffin et al. 2007b), that coyotes include marmots in their diets wherever the two species overlap in the park (Witczuk 2007), that the park comprises about 90% of the marmot's range, that even moderate changes in survival can translate to big changes in marmot population growth rates, and that coyotes were not historically present on the Olympic Peninsula (Houston et al. 1994a; Sheffer 1995), the most parsimonious explanation for the marmots' rangewide decline is coyote predation.

Although it is apparent that marmot survival rates have declined and that the current level of coyote predation is sufficient to considerably depress marmot population growth, it is unclear why coyote predation has recently become problematic and whether coyote control would improve marmot population growth. Coyotes have been present in the Olympic high-country since the 1940's (Johnson & Johnson 1952; Sheffer 1995). Coyote abundance since that time is unknown but anectodal evidence suggest that coyotes have become more common in recent years. In four years of marmot observations in the 1960's Barash saw coyotes only twice (D. Barash, personal

communication), whereas during 2002-2006 my assistants and I saw coyotes >30 times; in 2002, I personally saw coyotes on at least five occasions suggesting an increase in abundance. However, it is also possible that marmot behavioral changes or tree encroachment into meadows has made marmots more vulnerable to predation. The highest levels of marmot mortality were inflicted on adult females in June; their unique temporal and spatial foraging patterns associated with pregnancy and lactation (Barash 1980) likely predispose them to predation. Changes in temperature or seasonal distribution of forage linked to climate change could lead to these energetically stressed marmots foraging even more actively at dawn and dusk when predators are most active, or foraging nearer to the edges of meadows where vegetation is likely to contain more moisture and more cover is available for predators.

This leads to the question of whether marmot population growth rates would have decreased regardless of whether coyotes had become established in the high country. Coyote predation on marmots can only depress growth rates if that predation is additive to the background rate of predation and is not compensated for by increased rates of reproduction or juvenile survival (Nichols 1991). The dramatic results of an unreplicated "natural experiment" support the hypothesis that coyote predation is additive, as follows. From spring 2002 to fall 2003, the number of non-juvenile marmots in the Western site group declined from 22 to 14 and seven radio-tagged marmots died, at least four of which were definitively killed by coyotes (Appendix E). The survival rate for all radio-tagged marmots in the area during 2002 and 2003 averaged 0.61 (95% CI: 0.38, 0.93). In fall 2003, a coyote that was known to prey on marmots in the area was removed after it threatened a child. The following summer, the marmot survival rate jumped to 0.82 (0.59,

1.05). Furthermore, reproductive rates were actually higher in 2004 than in previous years and by spring of 2005 the Western population had rebounded to 20 animals. Further evidence comes from observations at the Central site group: From spring 2005 to fall 2006 coyotes were regularly sighted in this region and their scat was abundant with a high proportion containing marmot remains (Witczuk 2007). Marmot mortality was simultaneously high and marmot abundance fell from 44 to 27 marmots. The high mortality rates were not compensated for by increased reproductive output – in 2006, only one of five surviving females weaned a litter. At the Central site group during 2005-2006, high marmot mortality and a steep population decline were associated with frequent coyote sightings and marmot occurrence in coyote scats; high mortality was not compensated for by increased reproductive output. Although these observations do not prove that coyote predation is additive, they provide considerable support for this hypothesis.

The life-history traits of Olympic marmots are consistent with those seen in other species that experience low adult mortality, and it is likely that they evolved without heavy predation. Of the marmot species in which predation is well-documented, Olympic marmot life-history most closely resembles that of the Vancouver Island marmot, a species that is also experiencing high levels of predation (apparently resulting from landscape changes associated with industrial forestry). Relative to woodchucks (*M. monax*) and yellow-bellied marmots, both of which commonly live in areas with diverse predator communities, Olympic marmots mature late and breed infrequently. It is widely accepted that low reproductive rates are generally associated with high adult survival and with increased risk of extinction (Purvis 2000).

Coyotes and badgers are the most important terrestrial predators on yellow-bellied marmots in both Colorado (Van Vuren 2001) and Oregon (Thompson 1980). Both were historically absent from the Olympic Mountains. Instead, wolves, cougars, bobcats, and black bears would have constituted the terrestrial predator community. While wolves and cougars will opportunistically prey on marmots (Bryant & Page 2005), both specialize on ungulates (Currier 1983; Mech 1974). Wolves do not routinely take prey smaller than beavers (*Castor canadensis*) (Mech 1974). Cougars are typically nocturnal or crepuscular and approach their prey under cover. As diurnal, open-country inhabitants, marmots are not likely to encounter them frequently. Bobcats are known to prey on woodchucks (Lariviere & Walton 1997) but have not been reported as important predators on other species of marmots. Both cougars and bobcats have been reported to prey on Olympic marmots but inspection of predated marmots (this study) and analyses of carnivore scat (Witczuk 2007) suggest this is rare. Black bears prey occasionally on yellow-bellied marmots (Van Vuren 2001). However, bears are often seen foraging in close proximity to Olympic marmots without eliciting alarm calls, suggesting that they rarely prey on Olympic marmots.

As generalist introduced predators with a broad prey base in the Olympic Mountains (Witczuk et al., unpublished data), coyotes are unlikely to be significantly impacted by marmot declines (e.g., Prugh 2005). If coyotes continue to prey heavily on marmots as the marmot population declines, coyotes could drive Olympic marmots to extinction. Thus, there is justification for reducing or eliminating coyotes in Olympic National Park. Unfortunately, coyotes are notoriously difficult to control and virtually nothing is known about their population dynamics on the Olympic Peninsula, except that

they occur throughout the remote high-country (Witczuk 2007). A recent study in California has found that while coyote that live in the hills frequently dispersed downslope, movement the other way was non-existent (Sacks et al. 2004). If coyote movement on the Olympic Peninsula is equally asymmetrical and if the high-country is relatively unfavorable habitat for them, a periodic eradication program could be effective. On the other hand, if coyotes regularly move upslope or if population growth rates are high in the mountain population, control efforts may be near-futile.

Wolf reintroduction to the Olympic Peninsula is discussed periodically (Ratti et al. 2004), and given the publicity given early indications that reintroduced wolves altered coyote behavior and depressed coyote populations in Yellowstone (Berger & Gese 2007; Smith et al. 2003; Switalski 2003), the results presented herein will undoubtedly lead to renewed calls to reintroduce wolves to the Olympic Mountains. However, reintroduced wolves would be expected to settle primarily in the elk-rich western valleys (Ratti et al. 2004), whereas marmots are rare on the western slopes (Griffin et al. in review) and coyotes are abundant in the north and east. If the high elevation coyotes population in the Olympic Mountains is a sink, and if reintroduced wolves were to kill enough low-elevation coyotes to reduce the number of coyotes dispersing upslope, wolf reintroduction could reduce coyote levels. Whether or not this would be the case remains to be seen.

Although connected to mainland North America, in many ways the Olympic Peninsula resembles an island. The organisms that live in the Olympic Mountains have been confined to a relatively small amount of habitat, with a limited number of competitors and importantly, few predators, for millennia. The evolutionary experience

and current life-history of Olympic marmots predispose them to extinction when faced

with a non-native generalist predator, even within the confines of a national park.

FIGURES

Figure 1. Projected population growth rates, λ, for Olympic marmot (*Marmota olympus*) at each of three groups of study sites and the population average in Olympic National Park, 2002-2006, based on current birth and mortality rates (left-hand group of bars) and three scenarios for reduced mortality rates of non-juveniles. Shown are projected λ given a) current mortality rates, b) a 28% reduction in mortality (i.e., elimination of confirmed coyote predation), c) a reduction in mortality sufficient to result in a survival rate of 89% (1960's levels; Barash 1973), and d) a reduction in mortality by 88% (the maximum plausible portion of marmot mortalities caused by coyotes during 2002-2006). Coyote predation rates in this study were estimated based on a sample of radio tagged marmots and so have confidence intervals associated with them. The error bars on groups b and d indicate the range of λ's resulting from reducing the mortality rates across the 95% CI range of known and maximum possible coyote predation levels. Bars above the dotted horizontal line (i.e., $\lambda > 1.0$) indicate that the population would be expected to increase.

Figure 2. Assigned cause of mortality for 43 radio-tagged Olympic marmots. Results are shown separately for adult females ($n = 20$) and all other marmots (14 adult males and 9 subadults). The category "presumed predation" includes 5 cases that were determined to be predation by terrestrial carnivores and 7 cases that could have been predation by either terrestrial carnivores or raptors. "Missing" marmots were likely predated and the transmitter destroyed in the course of the predation event (see text).
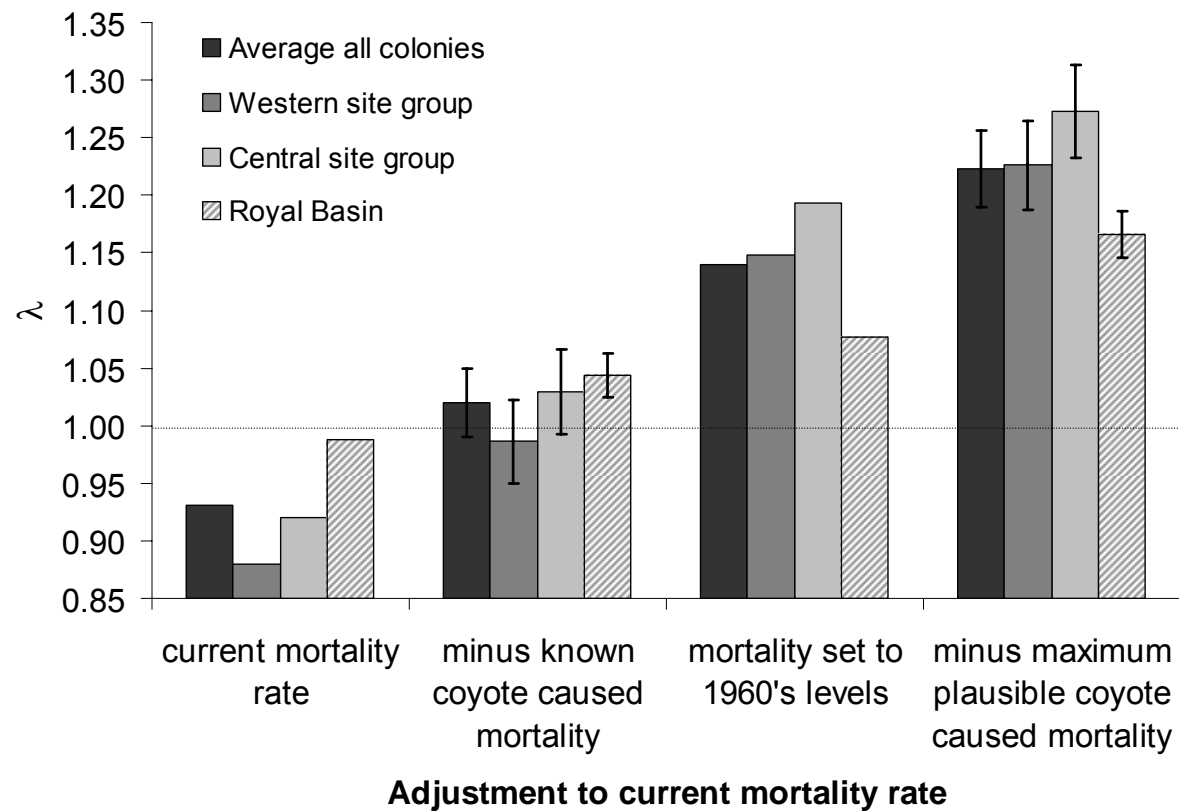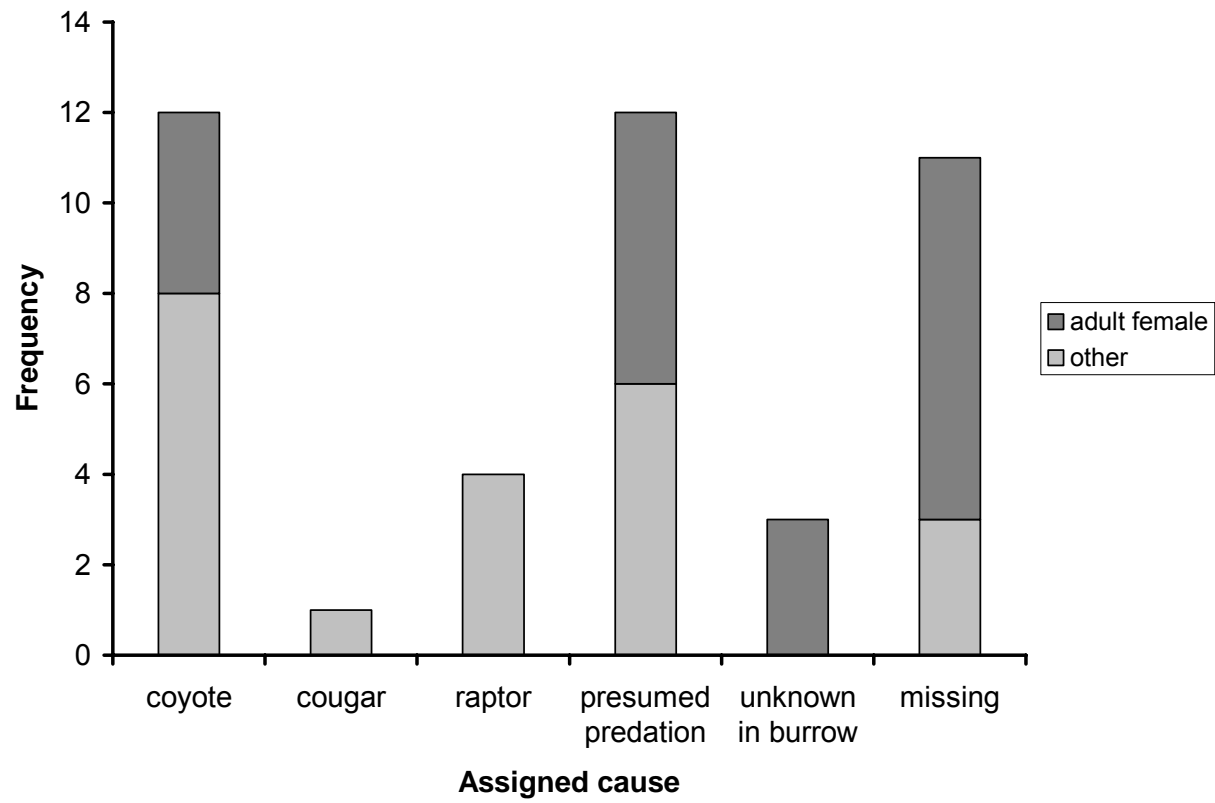
CHAPTER 5.

AN IMPROVED METHOD FOR DELINEATING HABITAT FROM PRESENCE DATA: OLYMPIC MARMOTS AS AN EXAMPLE

Abstract. Conservation of rare and management of overabundant species both depend in part on accurate prediction of potentially suitable habitat. Most habitat models rely on both presence and absence data but because the latter is not always available, approaches have been developed that require only presence data. The Mahalanobis distance statistic (D^2) has been successfully used to identify suitable habitat from presence data alone but there has been no mechanism to select among potential habitat covariates. We sought to use presence-only data to identify potentially suitable habitat for the Olympic marmot (*Marmota olympus*), a declining species endemic to Olympic National Park. We developed an approach to identify the best combination of explanatory variables that relies on ranking potential models based on the proportion of the entire study area that they classify as potentially suitable when a predetermined proportion of occupied locations are correctly classified. We were seeking, in effect, to minimize the error of commission rate or maximize specificity while holding the omission error rate constant. A seven variable model identified 21,143 ha within the park as potentially suitable for marmots, while simultaneously correctly classifying 80% of the occupied locations. An earlier "expert-opinion" based model, which admittedly was intended to err on the side of over-inclusion, identified 28,275 ha as potential habitat yet still failed to include all habitat. The earlier model had provided no way of ranking patches in terms of likely suitability. Additional refinements to the seven variable model (e.g., eliminating

small patches) further reduced the predicted area to 18,579 with little reduction in predictive power. Although we sought a model that would allow field workers to find 80% of Olympic marmot locations, < 3% of 376 occupied locations and < 9% of abandoned locations were > 100 m from habitat predicted by the final model, suggesting that >90% of locations could be found by observant workers surveying predicted habitat. The model comparison procedure allowed us to identify the best model structure, maximizing the specificity of our model and, thus, limiting the amount of less favorable habitat included in the final prediction area.

Key Words: *habitat model; Mahalanobis distance;* Marmota olympus; *Olympic marmot; Olympic National Park;*

INTRODUCTION

Accurate mapping of suitable habitat for organisms is critical to a range of conservation objectives. For example, implementation of a monitoring program for the Olympic marmot (*Marmota olympus*), a ground-dwelling squirrel that has undergone recent local extinctions (Griffin et al. in review), will require identification of both currently occupied and currently unoccupied but potentially suitable habitat (Witczuk 2007). Although habitat models are most often built using presence / absence data, several methods have been developed to predict distribution or rank potential habitat when absence data is unavailable, unreliable, or incomplete (Clark et al. 1993; Pearce & Boyce 2006), as it was for the marmot. The Mahalanobis distance statistic (D^2) has been successfully used to identify suitable habitat from presence data alone in several species

that had recently declined for reasons independent of habitat quality (Thompson et al. 2006; van Manen et al. 2005), for which only presence data was available (Boetsch et al. 2003; Clark et al. 1993; Corsi et al. 1999; Cuesta et al. 2003), or for which absence data was unreliable (Browning et al. 2005). It performed well in a recent comparison of presence-only models (Tsoar et al. 2007). However, its application has been limited, perhaps in part because there is no well-established method to determine which explanatory variables should be included in the final model (Johnson & Gillingham 2005, but see discussion of partitioned D2 below). We have developed an approach for identifying the best subset of explanatory variables to minimize overprediction of suitable habitat while correctly classifying a predetermined proportion of the occupied locations. We use our approach to develop a map of potential habitat for the Olympic marmot.

Mahalanobis distance models

The Mahalanobis distance statistic (D^2) represents the standard squared distance between the covariate values for a given sample and the mean vector of these covariates for the training data. In the context of habitat modeling, a D^2 value is computed for each map cell or pixel based on the value of the habitat covariates under consideration in that cell, relative to the average values of those covariates at the occupied locations. Cells with smaller D^2 values have habitat values more similar to the average occupied habitat, and so should be more likely to be occupied.

The D^2 values are continuous, with a minimum of 0. For the purposes of defining suitable habitat, a threshold D^2 value is typically identified after examining the distribution of the D^2 values of the cells containing the occupied training data (locations

used to build the model), test data (a portion of the original data set that was withheld when building the model, or data collected independently of that used to build the model. Map cells with D^2 values lower than that threshold are considered to be suitable for the study organism and the remaining cells unsuitable (Thatcher et al. 2006). The threshold may be set so that all occupied points are classified as being within suitable habitat (Boetsch et al. 2003; Podruzny et al. 2002), or such that some lesser proportion of the occupied locations are classified as suitable (Thatcher et al. 2006; Thompson et al. 2006; van Manen et al. 2005). The model is considered to perform well when the proportion of occupied pixels with D^2 values below the threshold is much greater than the proportion of random pixels with D^2 values below that same value (Browning et al. 2005; van Manen et al. 2005), or when the distribution of D^2 scores of occupied test locations is similar to those of the training data (Boetsch et al. 2003).

The D^2 statistic has several useful qualities. It does not assume multivariate normality in the habitat data (Knick & Dyer 1997), it specifically accounts for covariance among habitat covariates (Knick & Dyer 1997), and it is computed using only presence data (Clark et al. 1993). However, there are some disadvantages to D^2 as a tool for modeling habitat. First, we know of no statistical goodness-of-fit tests, although model fit can be qualitatively evaluated against null models or test data as described above (Boetsch et al. 2003; Podruzny et al. 2002) or evaluated with cross-validation procedures (Thatcher et al. 2006; Thompson et al. 2006). Second, there are no probabilities associated with the unscaled D^2 values. These values only rank the habitat in terms of suitability rather than providing a probability of occupancy for each map cell or pixel. Follow-up surveys guided by model predictions can provide estimates of probability of

occupancy if desired (Boetsch et al. 2003). Perhaps most importantly, there are no significance tests or other established methods of evaluating the importance of the explanatory variables (Johnson & Gillingham 2005). While other habitat modeling approaches (e.g., general linear models) allow stepwise inclusion and exclusion of variables, or permit comparison of how well several competing models fit the data at hand, we are unaware of any metrics that evaluate the effects of individual variables on the specificity of the D^2 statistic. This poses a particular problem because inclusion of extraneous or redundant variables may actually reduce the specificity of the model.

Several recent papers (Browning et al. 2005; Dunn & Duncan 2000; Rotenberry et al. 2006) have argued that it is possible to identify the variables that are most constant and therefore, useful predictors of habitat by partitioning the variance in the D^2 into the principle components of the correlation matrix. The variables that contribute most heavily to the eigenvectors with the smallest eigenvalues are considered to be important predictors of habitat. There are several apparent weaknesses in this decomposition approach. At a fundamental level, these eigenvectors will be more poorly estimated than the eigenvectors associated with the larger eigenvalues. Browning et al. (2005) attempted to account for this weakness by bootstrapping their data and eliminating several apparently unstable eigenvectors. Second, small variance components will arise when two or more variables are highly correlated, regardless of their importance to the organism (Steve Cherry, unpublished manuscript). Even if these statistical factors were unimportant in a particular situation (i.e., a very large data set with little or no correlation in the explanatory variables), the use of only the smallest k principle components can result in the prediction of considerably more habitat than would be predicted by a full

model (Rotenberry et al. 2006, figures 1 and 2). While what Rotenberrry et al. (2006) refer to as "niche" identification may contribute to theoretical understanding of a species' biology and perhaps potential range, reducing overprediction (increasing specificity) is one objective of most habitat modeling efforts.

The Olympic marmot

The Olympic marmot is a large, ground-dwelling squirrel endemic to the Olympic Peninsula. Since 1999, Olympic National Park's Resource Management Plan has called for determining the present distribution of marmots within the park and developing a long-term monitoring program for the species. A rigorous monitoring program and any future management program will hinge on the development of a valid habitat distribution model.

Beginning in 2002, we undertook a range-wide survey of potential Olympic marmot habitat (Griffin et al. in review), recording both presence and absence in several hundred polygons selected through a stratified random sample. We intended to use the polygons as the sampling unit in a resource selection function model but after initiating the survey we identified several limitations to their utility. In particular, the largest polygons exceeded >200 ha and encompassed many types of habitat. Marmots might occupy only a small portion of a given polygon but our survey protocol did not include differentiating used and unused portions within a polygon. By classifying the entire polygon as occupied in such cases, we would have designated large areas of unoccupied and possibly unsuitable habitat as occupied. Furthermore, our detection probability was less than one (Griffin et al. in review; Witczuk 2007), so some occupied habitat might

have been classified as unoccupied. Together these would have led to a considerable amount of misclassified habitat, violating one of the primary assumptions of presence / absence models. Furthermore, we had found marmots outside of polygons in numerous places – using only the polygon data would have resulted in an incomplete description of marmot habitat.

Thus, we sought a modeling approach that relied only on presence data and that could easily be applied to a large area in a geographic information system (GIS). The D^2 appeared promising but we believed that it was important to identify the most useful subset of explanatory variables. In particular, we compared models comprised of each possible subset of explanatory variables, seeking the combination that predicted the smallest proportion of the landscape as suitable given that 80% of the occupied locations were correctly classified as suitable. The 80% threshold was somewhat arbitrary but this definition provided us with a quantitative metric with which to compare models. Because the performance of any given model may depend on the particular sample of presence points, we compared the mean of the metric from 2500 bootstrap replicates from our presence data, rather than the results of a single sample. Finally, we used the best performing model to rank Olympic marmot habitat.

MATERIALS AND METHODS

Study system

The Olympic marmot is endemic to the Olympic Peninsula in northwest Washington State, USA. The Olympic Mountains, which reach 2400m, are completely isolated from the mountains on the mainland by water on three sides of the peninsula and

extensive lowlands to the south. Old-growth coniferous forest dominates at low and mid-elevations, while subalpine and alpine meadows, rock, and snow and ice cover the upper slopes. Heavy winter snows and spring rains feed 11 major rivers that bisect the landscape in deep, steep-sided valleys. The majority of high-elevation terrain is protected within the 3700 km^2 Olympic National Park. Ninety-five percent of the park is further protected as designated wilderness.

Olympic marmots are found on the upper slopes of these mountains, although they are relatively rare in the southwest (Griffin et al. in review). Like other alpine dwelling marmots, the Olympic marmot inhabits alpine and subalpine meadows, often interspersed with talus or rock outcrops, on moderately steep, south-east to south-west facing slopes (Allaine et al. 1994; Armitage 2000; Barash 1989a). The animals dig extensive burrow systems, which are used for multiple generations (Armitage 2000), and so require well-developed soil. Olympic and other alpine-dwelling marmots are likely restricted to high-elevations both by the distribution of meadows and their intolerance of high temperatures (Melcher et al. 1990; Türk & Arnold 1988). Visibility may contribute to suitability of meadows, presumably as it influences predator detection (Blumstein et al. 2006; Borgo 2003). However, these habitat requirements are generalities – we have found Olympic marmots on all aspects, a wide range of slopes, and at the edge of forests.

Definition of study area

Marmots are found throughout the upper reaches of the peninsula, but GIS cover-type data was restricted to Olympic National Park and a 1.5 km buffer so our study was restricted to this region. Practically, this included almost the entire range of the species as

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>90% of the range is within the park and most of the remaining is immediately adjacent to it. We further restricted our study area to regions above 1300m. This elevation cut-off is lower than that used in the 2002 model (see below) and represents the elevation of the lowest known marmot colony. Finally, we removed all pixels classified as 71-100% closed canopy in the cover-type layer, as marmots are not found in closed canopy forest.

Collection of location data

From 2002-2005, we surveyed 811 polygons of possible marmot habitat throughout Olympic National Park. These polygons were identified in a preliminary GIS model (hereafter, the 2002 model) and polygon selection and survey protocol are described in detail elsewhere (Griffin et al. in review). Briefly, patches of meadow or rock (a cover class that included bare ground) >1400 m were subdivided by aspect and patches < 0.56 ha were removed as they were believed to be too small to support marmots. Groups of one to five of the resulting polygons were surveyed according to a stratified random sampling design. Polygons were classified as occupied, abandoned, or without sign of marmots (no sign) based on the presence of marmots, active or inactive burrows, and other evidence. In most cases, when marmots or burrows (active or abandoned) were found, representative locations were taken with a handheld GPS unit (usually accurate to ±10 m). From 2001-2006, marmots or burrows opportunistically found outside the polygons were recorded, and several written and oral reports of marmots were investigated. During 2002-2005, we also conducted intensive trapping, resighting, and radiotelemetry studies in three areas of the park (Griffin et al. 2007b), and

we collected hair samples for genetic analyses from marmots throughout the park. During each of these activities, additional location data were collected.

The total number of occupied locations from all sources was >10,000. Over 5000 of these came from our intensive study sites, and many locations represented multiple records of the same burrow. In an effort to use as many of the data as possible without over-representing the intensive study areas, we subsampled from the original data set. We randomly selected points, eliminating those that were <125 m from a previously selected point, until all points were either selected or eliminated from consideration. The 125-m buffer was chosen to approximate the habitat available to or used by a typical marmot, as the median MCP home range of Olympic marmots is 4.59 ha ($n = 47$; unpublished data). We also selected a sample of points using a 200-m buffer to explore the effect of buffer size on the distributions of the habitat covariates. Locations from three colonies that became abandoned during the course of the four years were included in the occupied data set. We removed eight locations that fell within pixels classified as 71-100% canopy closure as these were likely the result of GPS or recording error, and they fell outside the defined study area. Following subsampling, the marmot presence data set was comprised of 376 occupied points.

In addition to the occupied locations, we recorded the locations of abandoned burrows. Additional support for the model would be provided if it predicted abandoned locations to be suitable habitat, although differences in the occupied and abandoned locations could indicate differences in the two types of sites, rather than a poorly fitting or overfit model. Abandoned locations were restricted to burrows that showed no signs of recent use and that were located in areas that either contained many such burrows or

where there were historical records of marmots. Abandoned burrows were located during either the systematic surveys or targeted surveys. We screened out burrows that were in the vicinity (<200 m) of occupied habitat and any others that we felt might not represent truly abandoned habitat, initially leaving 175 abandoned burrow locations. We subsampled from these as described above to remove points < 125 m apart. After subsampling, 114 abandoned points remained.

Habitat covariates

Habitat models included up to 11 explanatory variables that described topography and vegetation within either the focal 25-m x 25-m pixel or a 25-pixel window centered on the focal (Table 1), depending on the scale at which we considered they might be important. For example, considering the proportion of pixels that were meadow or rock within a 25-pixel window rather than individual pixels, we intended to allow the inclusion of small sparsely vegetated or rocky areas if appropriate while penalizing those pixels that were surrounded by extensive rock or scree with no forage or digging substrate available. The use of the larger moving window would also have served to reduce the influence of classification error in the GIS-layer. On the other hand, continuous variables such as elevation and aspect should be adequately characterized by value of a single pixel. We attempted to use Beer's transformations (Beers et al. 1966) to linearize aspect but the result was a bimodal distribution. A bimodal distribution is not desirable for the Mahalanobis distance calculations because locations at the modes are relatively far from the mean and thus penalized, although the modes represent the most typical locations for marmots. Instead, we used two binary variables, NE/SW and

NW/SE, to describe aspect. We used northeast vs. southwest rather than north vs. south because northeast is generally the coldest aspect and southwest the warmest. We thought that marmots might use some types of meadow more than others and considered including separate variables for the proportion of each of the five meadow types identified in the GIS-cover type layer within the 25-pixel window as separate variables. However, the relative rarity of each class resulted in the mean proportion of the window occupied by each class being small (< 0.10). Thus, locations with a high proportion of any given meadow type would have been penalized because they were unusual although larger amounts of meadow are presumably good for marmots (the best habitat is rare in this case and so not represented by the average of the occupied locations). Therefore, we chose not to include separate variables for each of the 5 meadow types but rather lumped all together into a single classification of meadow.

Comparison of Mahalanobis distance models

The D^2 statistic is calculated for each map cell in a study area as follows:

$$D^2 = (\hat{\underline{\mu}} - \underline{x})' \hat{\Sigma}^{-1} (\hat{\underline{\mu}} - \underline{x}),$$

where $\hat{\underline{\mu}}$ is the vector of the mean values and $\hat{\Sigma}$ is the variance-covariance matrix of some number of habitat covariates at the presence locations. $\underline{x}$ is the vector of values for each habitat variable for a given cell. Small values, close to zero, indicate habitat most similar to the average of the occupied cells. If the assumption of multivariate normality is met in the training data, then the D^2 values are chi-square distributed and can be rescaled to probabilities, as was done by Clark et al. (1993). Even when this assumption is violated, as it was in our case, there is a monotonic relationship between the D^2 values

and dissimilarity from the mean, with equal scores being equally distant from the mean in multivariate space.

Our objective was to compare the ability of each of the 2047 possible models (2^{11} – 1 combinations of 11 habitat covariates) to accurately identify a high proportion of suitable habitat while minimizing the amount of the total landscape predicted. Determining D^2 values for an entire landscape of hundreds of thousands or millions of map cells requires the use of GIS software, making it cumbersome to compare the results of a large number of models. However the D^2 values of a smaller subset of locations can be efficiently calculated for many models using Matlab (MathWorks 2005) or similar software. Therefore, we randomly selected 1000 map cells from within the study area to represent the total landscape in our comparisons. The 376 presence locations, or bootstrapped samples from the presence locations, served to represent suitable habitat.

As a metric with which to rank the models, we determined the proportion of the random locations that would be classified as suitable habitat under each of the models given that 80% of the occupied locations were classified as suitable (we term this metric P_{r80}). That is, for each model we identified the smallest D^2 value such that 80% of the training data (in this case, the bootstrap sample of 376 presence locations) fell in map cells with values less than or equal to that value. All map cells with equivalent or smaller D^2 values were classified as suitable, and cells with larger D^2 values were classified as unsuitable. Models could then be ranked based the P_{r80}, with lower values indicating superior models for our purposes. We were, in effect, seeking to minimize the error of commission rate or maximize specificity while holding the omission error rate constant at 20%. The 80% threshold for defining suitable habitat was somewhat arbitrary and the

optimal point of comparison will vary depending on the purpose of the model. Others have used as a cut-off for suitable habitat the D^2 value at which difference in the cumulative frequency of the occupied and random points is greatest as a threshold for identifying suitable habitat (Thatcher et al. 2006; van Manen et al. 2005).

Because $\hat{\underline{\mu}}$, $\hat{\Sigma}$, and ultimately P_{r80} for a given model depends on the particular sample of presence points, we compared the mean of this metric from 2500 bootstrap replicates of size 376 from our presence data, rather than the results of a single sample. We calculated P_{r80} for each replicate under each of the 2047 models based on $\hat{\underline{\mu}}$ and $\hat{\Sigma}$ for that bootstrap sample. We ranked all 2047 models based on $\overline{P}_{r80}$.

To determine whether the random points predicted to be suitable differed greatly from model to model, we calculated the Sorenson's similarity coefficient (Ssc, Sorenson 1948) between the top model and each of the other models. This statistic measures the degree of overlap in two groups, with a value of 1 indicating total overlap (e.g., all points classified identically by the two models) and a 0 indicating that there is no overlap in classification. Matlab code for calculating the D^2 scores and P_{rX} from bootstrapped samples and for calculating the Ssc values is available in Appendix F.

For the highest ranked model based on the bootstraps, we built a single model from all 376 points. With this model, we computed the D^2 scores for abandoned burrows and 1000 random points selected from unoccupied polygons, and visually compared the cumulative frequency curves of each of these to that from the occupied data. Similarity between the abandoned and occupied data would provide additional support for the model, although differences in the occupied and abandoned locations could indicate differences in the two types of sites, rather than a poorly fitting or overfit model. Finally,

we randomly selected 1000 locations from the unoccupied polygons and compared the cumulative frequency curves of these to the occupied locations. Although these unoccupied locations were only drawn from a subset of the study area, they do provide an interesting comparison as they represent open, high elevation habitat that did not show any sign of recent marmot use. If the Mahalanobis distance model represented a substantial improvement over the 2002 model upon which we based our surveys, a large proportion of these unoccupied points should be classified as unsuitable.

Final model refinements and evaluation

The best performing model was used to produce a final habitat map for Olympic marmots. We used the $\hat{\mu}$ and $\hat{\Sigma}^{-1}$ from all 376 occupied locations to compute D^2 values for each pixel in the entire landscape. For this purpose, we wrote an ALM code for use in ARC/INFO GIS (ESRI, Redlands, California, USA). We identified the D^2-value at which 80% of the 376 occupied locations were correctly classified and used this as the upper limit for designating habitat as suitable for Olympic marmots.

We then made several additional refinements to facilitate comparison with the 2002 habitat model and to make the final model more useful for Olympic Park monitoring and management efforts. First, we eliminated several patches of permanent snow and ice that were predicted as they are clearly inhospitable to marmots. Second, as in the 2002 model, we removed patches of predicted habitat < 0.56-ha, assuming them to be too small to support marmots. Finally, we eliminated the areas outside the park boundaries as the 2002 model did not include these areas and monitoring by park personnel would be confined to the park.

We then determined the distance that each occupied and each abandoned location fell from predicted habitat in this refined model so as to confirm that the removed patches were not important marmot habitat. This also allowed us to determine whether or not the points falling outside the predicted area were at least in close proximity to these areas. We also examined the amount of rock predicted by our new model as one objective of the modeling process had been to eliminate some of the 20,454 ha of often inhospitable rock that were identified as habitat by the 2002 model.

RESULTS

Study area and location data

The final study area encompassed 78,302 ha of open or lightly wooded, high-elevation terrain within or immediately adjacent to Olympic National Park. Although the 376 occupied points (figure 1) that remained after subsampling were not selected randomly, they should be generally representative of marmot habitat throughout the park. Seventy-five percent of known occupied polygons (165 of 219) were represented by one or more locations in the sample. There was no indication that 165 polygons represented in the sample differed from the 54 that were occupied but not represented with respect to region, aspect, area class or slope class (X^2 tests, all $P > 0.05$). Points outside the polygons constituted 12% of the data set – these by definition differed from the other occupied points as they did not fit the original criteria for inclusion as potential habitat. Similarly, after subsampling 114 abandoned locations remained. These were in or near 78 of the 111 (70%) of the polygons that were classified as abandoned. Increasing the buffer-size from 125 m to 200 m resulted in a 31% reduction in the number of cases

available with no significant statistical or biological differences in the distributions of the 11 habitat covariates. We took this to indicate that the 125-m buffer adequately reduced the influence of the most intensive study sites.

Model comparison

We compared $\overline{P}_{r80}$, the mean proportion of random locations predicted to be suitable habitat, from 2500 bootstrap replicates for 2047 models representing all possible combinations of 11 habitat covariates. A model with seven covariates (Table 2) performed the best of this set, with 29.2% of the random locations predicted to be suitable. Of the 2500 bootstrap replicates, this seven variable model was top ranked in 624 (25%). For all other variable combinations, $\overline{P}_{r80}$ was greater than 30% (Figure 2) and the full model ranked 8th with a $\overline{P}_{r80}$ of 30.8%. The bootstrap replicates demonstrated that there was considerable variability in the proportion of the random locations classified as suitable due to sampling. The 5th and 95th percentiles of this distribution for the top ranked model were 25.3% and 33.6%. This range of variability was lower than for 92.9% of the 2047 models.

Several covariates appeared at high frequency in the top 100 models (Table 2). Elevation proved to be the most critical – appearing in the top 459 models. Rock, meadow, and May insolation each appeared in > 90 of the top 100 models. These were followed in apparent importance by aspect NE/SW, aspect NW/SE, and profile curvature. Slope, planiform curvature, trees and sd of slope all appeared in < 55 of the top ranked 100 models. The top ranked model included only the seven most frequently occurring covariates.

A model's Sorensen's similarity coefficient to the best model (Ssc) generally decreased with model rank (Figure 3), but there was considerable variation in scores even among models that predicted almost the same proportion of the random points to be suitable. This indicates that although the highest ranked models all predicted about 30% of the random points to be suitable habitat, not all of these highly ranked models predicted similar map cells to those predicted by the top-ranked model. In particular, it appeared that the inclusion of trees as a predictor variable led to greater dissimilarity in the configuration of selected habitat (Figure 3).

The cumulative frequency curve for the occupied locations showed a high degree of overlap with the abandoned locations (Figure 4). The cumulative frequency curve for points selected from the unoccupied polygons lay considerably below that of the occupied and abandoned locations and only 37% of these had D^2 values less than the threshold vale of 8.54.

Final model refinements and evaluation

The unrefined final model (figure 6), built using seven habitat covariates and all 376 occupied locations, identified 22,624 ha (28.9% of the entire study area) as containing 80% of the suitable habitat ($D^2 < 8.54$). Within the park itself, 21,143 ha had D^2 values ≤ 8.54; when snowfields and polygons < 0.56-ha in area were removed, the predicted area was further reduced to 18,579 ha. It is this area that is comparable to our 2002 model, which was similarly restricted to the patches > 0.56-ha within the park but predicted 28,275 ha.

The elimination of the small patches did little to reduce the specificity of the model. Of the 376 occupied locations, 77.7% fell within predicted habitat and only 2.7% were > 100 m from this area. Of the abandoned locations, the corresponding percentages were 71.9% and 7.0%. Only 4,653 ha of rock were classified as suitable for marmots in our new model, as compared to 20,454 ha identified as potential habitat in the original model. However, the reduction in overprediction of rock came with a cost – 6.575 ha of trees were predicted as suitable in the final model, whereas treed pixels were excluded from the 2002 model.

DISCUSSION

Mahalanobis distance based models are useful for predicting species occurrence but their application has been limited in conservation and ecological studies. Without a formal approach to variable selection, decisions about what variables to include in a final model had to be made based only on expert opinion or by experimenting with different combinations. As inclusion of redundant or uninformative variables can actually reduce the specificity of the model, this represented an important limitation on the use of the Mahalanobis distance to model habitat. Partitioning the variance in the data set has been proposed as a way to identify important variables (Browning et al. 2005; Dunn & Duncan 2000; Rotenberry et al. 2006), but these methods are have statistical and practical weaknesses when used to model habitat.

In this paper, we have presented a simple approach for selecting among a set of possible habitat covariates to identify the subset with the highest discriminatory power. We successfully applied our approach to occupancy data of Olympic marmots, creating a

useful habitat model with seven explanatory variables that outperformed a more complicated model with 11 variables.

Model comparison procedure

Our model comparison procedure allowed us to overcome a major limitation of the Mahalanobis distance statistic as a means of modeling habitat – the lack of robust and practical variable selection procedure. Including even a single extraneous or redundant variable greatly increases the number of parameters that must be estimated in the covariance matrix, and so reduces the precision of each estimate, lessening the reliability of the final model. Furthermore, because the Mahalanobis distance statistic only identifies how dissimilar any given location is to the average occupied location considering all the habitat variables, inclusion of variables that do not differ in distribution between occupied locations and the rest of the study area will "dilute" the distinctions between the two types of locations by inflating the within group variance relative to the between group variance.

For our data set, the comparison process indicated that to obtain the highest specificity (that is, minimize $\overline{P}_{r80}$) in identifying habitat, only seven of the original 11 habitat covariates should be used. Only a handful of models approached the top model in specificity and most were similar in structure to the top model, indicating that the comparison procedure had identified the most useful variables. The inclusion of trees in several of the top models did represent a deviation from this pattern. In particular, models including trees tended to predict somewhat different habitat configurations from models without trees, as indicated by relatively low Ssc values for those models. However, the

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highest ranked model outperformed the others (including those with trees) in multiple metrics. There was no indication that this model overfit the data, as the cumulative frequency curve of the abandoned data was almost identical to that of the training data. These abandoned locations included many mountains or ridge systems not represented in the occupied data set, and generally further south and west than the occupied location.

The model comparison procedure was able to identify a model that we would not have reached on our own, as it allows the covariance among the explanatory variables, and thus the amount of additional information each variable brings to the model, to be considered much more efficiently than casual inspection can do. While several variables were obvious candidates for inclusion – for example meadow, on which marmots have a well-established and obvious dependence (Armitage 2000; Barash 1989a) or May insolation, for which there were large differences between the means and variances of these variables at occupied and random locations (table 2) – the inclusion or exclusion of others were less obvious. Based only on observed differences in the distributions of occupied and random locations, we would probably have included trees but not aspect NW/SE. However, the model comparison procedure identified trees as less informative, while aspect NW/SE was included in the top model and 78 of the top 100 models.

It is important to recognize that while the computation of the D^2 statistic is independent of choice of study area, our model comparison metric is not. If, for example, our study area was the entire park, it is probable that the top-ranked model would have included trees as a predictor, as the majority of the park is forested. In order to produce the most specific model possible, we advocate defining the study area as narrowly as can be biologically justified – in our case, this meant that we placed a lower limit on

elevation and removed heavily treed pixels from consideration. Without the *a priori* removal of pixels with closed canopy from the study area, it is probable that trees would have been included in all the top models. The habitat identified as suitable by each model would not have changed but the models would have ranked differently. Strictly speaking, our efforts might have benefited if we had confined our initial study area to the park but given that there are marmots outside the park that may be of management interest in the future, it was reasonable to include that area.

Olympic marmots

The final habitat model appears to successfully identify suitable habitat for the Olympic marmot, based on quantitative criteria discussed above, as well as more qualitative criteria. In addition to accurately identifying the currently occupied locations used in building and testing the model, it identified as suitable most of the abandoned areas of which we are aware and several areas that we haven't surveyed but which backcountry travelers have told us might contain marmots or suitable habitat. Although only 80% of the 376 known marmot locations fell within the predicted habitat, most of the remaining were close enough that the marmots would likely be detected in a survey of the area. The variables included in the best model are biologically meaningful, and several have been previously suggested as being important to marmots.

In addition to being useful in its own right, the D^2 model is a considerable improvement upon the 2002 "expert-opinion" based habitat suitability model. Although the study area as defined for the current model included a much wider range of elevations than the original model, the final model identified considerably less of the landscape to

be suitable. After removal of snowfields, patches < 0.56 ha, and areas outside the park, 18,579 ha was predicted area to hold 77.7 % of the marmot population. The "expert-opinion" based model, which admittedly was intended to err on the side of over-inclusion, identified 28,275 ha as potential habitat yet still failed to include all habitat. It provided no way of ranking patches in terms of likely suitability. Importantly, the final model predicted substantially fewer rock / sparsely vegetated pixels as potential habitat. While marmots will use talus and the sparsely vegetated terrain that they often use classifies as rock in our cover-type layer, they do require some vegetation and are not found on the expansive rock outcrops, cliffs, and recently glaciated areas common in the Olympic Mountains. By considering the proportion of pixels that were meadow or rock within a 25-pixel window rather than individual pixels, we intended to allow the inclusion of small sparsely vegetated or rocky areas if appropriate while penalizing those pixels that were surrounded by extensive rock or scree with no forage or digging substrate available. The use of the larger moving window would also have served to reduce the influence of classification error in the GIS-layer.

The final model did predict lightly forested areas more often than we would have preferred, although marmots are found close to or in lightly treed areas on occasion. In the original 10,000 locations, there were undoubtedly poor GPS fixes and transcription errors, as well as marmots that were in atypical habitat. Although we believe that these errors were rare and we removed the most obvious ones, the subsampling process by which we reduced our initial database of presence locations to 376 would have increased their frequency in the data set. The errors that resulted in presence data being located in inappropriate habitat were likely to result in those locations also being >125 m from other

occupied locations – thus, these erroneous and misleading points would have been retained during the subsampling. We considered using only hibernacula locations (Borgo 2003), or hibernacula and natal burrows, but our data for these are restricted to the northeast and the sample sizes are limited. We also considered removing all locations that were in pixels classified as treed but we knew many of these to be valid. The 4th ranked model, which included trees as a variable, identified many fewer treed pixels as suitable but at the cost of identifying many more areas of rock and talus. Although the top-ranked model represented only a small improvement in specificity over the 4th-ranked model, practically it represents a considerable improvement. Rock and talus are more difficult to survey than forest so the inclusion of extraneous trees poses a smaller future cost to the monitoring program than the inclusion of extraneous rock and scree.

Conclusions

The choice of a modeling approach for identifying suitable habitat for a species may be dictated by quantity, quality, and type of distribution data, availability and scale of GIS layers, the intended use of the resulting map or maps, the flexibility of the modeling approach, and even the skill set of the practitioner. Given limitations in our data set and our intended objective of identifying locations suitable for a monitoring program, the Mahalanobis distance approach seemed appropriate. The model comparison procedure allowed us to identify the best model structure, maximizing the specificity of our model and thus, limiting the amount of less favorable habitat included in the final prediction area. We expect the Mahalanobis distance and other presence only approaches

to modeling habitat will see increased use as identifying suitable habitat for an increasing number of declining species becomes ever more important.

Table 1. Names and descriptions of variables used in developing habitat models for Olympic marmots.

Table 2. Means (standard deviations) at all occupied locations (n=376) and random points within the study area (n=1000) of explanatory variables, the number of times that each variable appeared in the highest ranking 100 models, and the whether or not the variable was included in the final habitat model for Olympic marmots.

Table 1.

Variable	Description (units)	Classes or value range	Window
Elevation[27]	Elevation (m)	1300 – 2,430	Focal pixel
Slope[28]	Slope steepness (degrees)	0-89	Focal pixel
Rock[29]	No. of rock / sparse ground pixels within window	0 - 25	25-pixel
Meadow[3]	No. of meadow pixels within window	0 - 25	25-pixel
May insolation[30]	Modeled incoming daily solar radiation for May 21 (10^6 Kj m^{-2})	23.0 – 41.1	25-pixel
Aspect NE / SW[2]		0 / 1	Focal pixel
Aspect NW / SE[2]		0 / 1	Focal pixel
Tree[3]	Trees present within focal pixel	0 / 1	Focal pixel
SD of slope[2]	Measure of topographic variability (standard deviations)	0.7 – 21.0	25-pixel
Planiform Curvature[2]	Slope curvature in horizontal plane (unitless)	-24.6 – 30.8 (4)	25-pixel
Profile Curvature[2]	Slope curvature in vertical plane (unitless)	-20.6 – 18.4 (4)	25-pixel

[27] National Elevation Dataset. 1/3 arc-second U.S. Geological Survey (USGS), EROS Data Center. 1999.
[28] Derived from 1.
[29] National Park Service. Pacific Northwest Region Vegetation and Landform Database Development Study. Pacific Meridian Resources. 1996.
[30] Hetrick, W. A. , P. M. Rich, and S. B. Weiss. 1993b. Modeling insolation on complex surfaces. *Thirteen Annual ESRI User Conference*, Volume 2, pp. 447-458.

Table 2.

Variable	occupied locations $\overline{X}$ (SD)	Proportion of occupied locations	random locations $\overline{X}$ (SD)	Proportion of random locations	No. times included in top 20 models	No. times included in top 100 models	Included in top-ranked model?
Elevation (m)	1680 (119)		1594 (194)		20	100	Yes
Slope (°)	25.37 (11.18)		30.55 (11.71)		8	53	No
Rock	6 (7)		8 (9)		20	93	Yes
Meadow	10 (8)		4 (6)		20	99	Yes
May insolation	37.32 (3.06)		35.64 (4.39)		20	91	Yes
Aspect NE/SW		0.37 (north)		0.48 (north)	19	65	Yes
Aspect NW/SE		0.56 (east)		0.57 (east)	20	78	Yes
Tree		0.18 (with trees)		0.33 (with trees)	8	50	No

SD of slope	5.60 (2.90)	5.75 (2.94)	9	44	No
Planiform Curvature	-0.82 (6.10)	-0.03 (7.67)	7	38	No
Profile Curvature	0.88 (10.14)	-0.37 (12.63)	15	62	Yes

FIGURES

Figure 1. Polygons of habitat (gray shading) within Olympic National Park known to be occupied by Olympic marmots (*Marmota olympus*) and 376 point locations (black triangles) used in development of habitat models for the species. The intensive study sites are circled. Polygons known to be abandoned (gray shading) and the abandoned point locations (black triangles) used to test the habitat model are shown in the inset.

Figure 2. Mean percentage of locations randomly selected from study area that were classified as suitable (with the 5th and 95th percentiles of the 2500 bootstrap samples) by each of the 2047 models, ordered in descending order of performance. The top fifty models are shown in the inset.

Figure 3. Sorenson's similarity coefficient (Ssc) relative to the top-ranked model for all models that included trees (black crosses) and did not include trees (gray squares). The gray line indicates the maximum possible value for each model, given the proportion of the random points classified as suitable by the top model and the model under consideration.

Figure 4. Cumulative frequency curves of Mahalanobis distance (D^2) values for Olympic marmot from the highest ranking of 2047 models. See the text for explanation of four types of location data.

Figure 5. Relative suitability of habitat for Olympic marmots within and adjacent to Olympic National Park based on the Mahalanobis distance (D^2) scores from the unrefined top-ranked model. The habitat most similar to the average of the occupied locations is shown in black, with progressively lighter gray indicating increasing dissimilarity.

Figure 6. Predicted distribution of suitable habitat for Olympic marmots (dark gray), based on the top-ranked, seven-variable model, clipped to the extent of the park, from which snowfields and patches < 0.56 hade been removed. Also shown are additional areas predicted by the 2002 model that were not predicted by the current model (light gray) and the 376 occupied locations used to build the model (black triangles). A number of the abandoned locations used in evaluating the fit of the model are also shown in the inset (black crosses); > 90% of both abandoned and occupied locations fell within 100m of the predicted habitat.
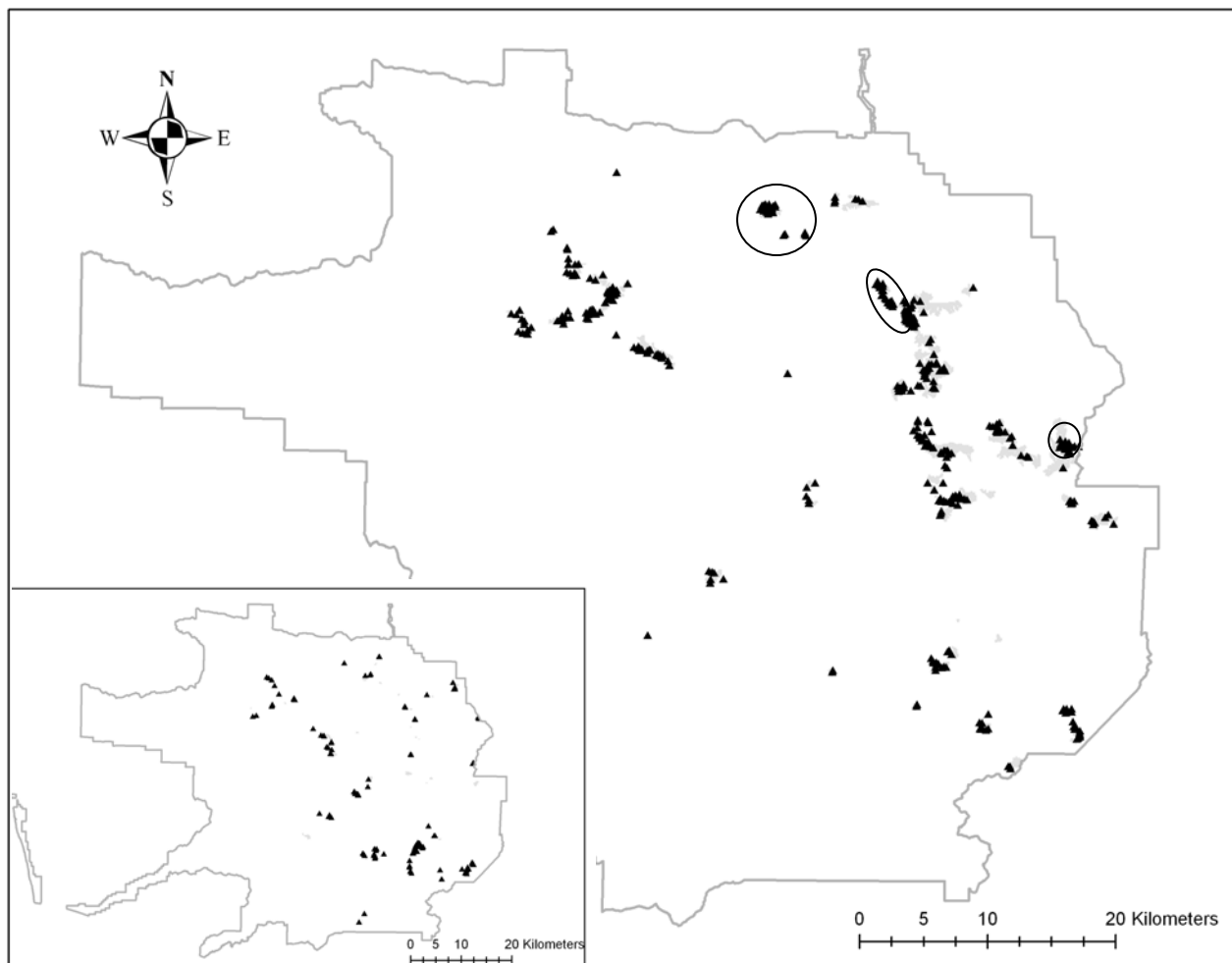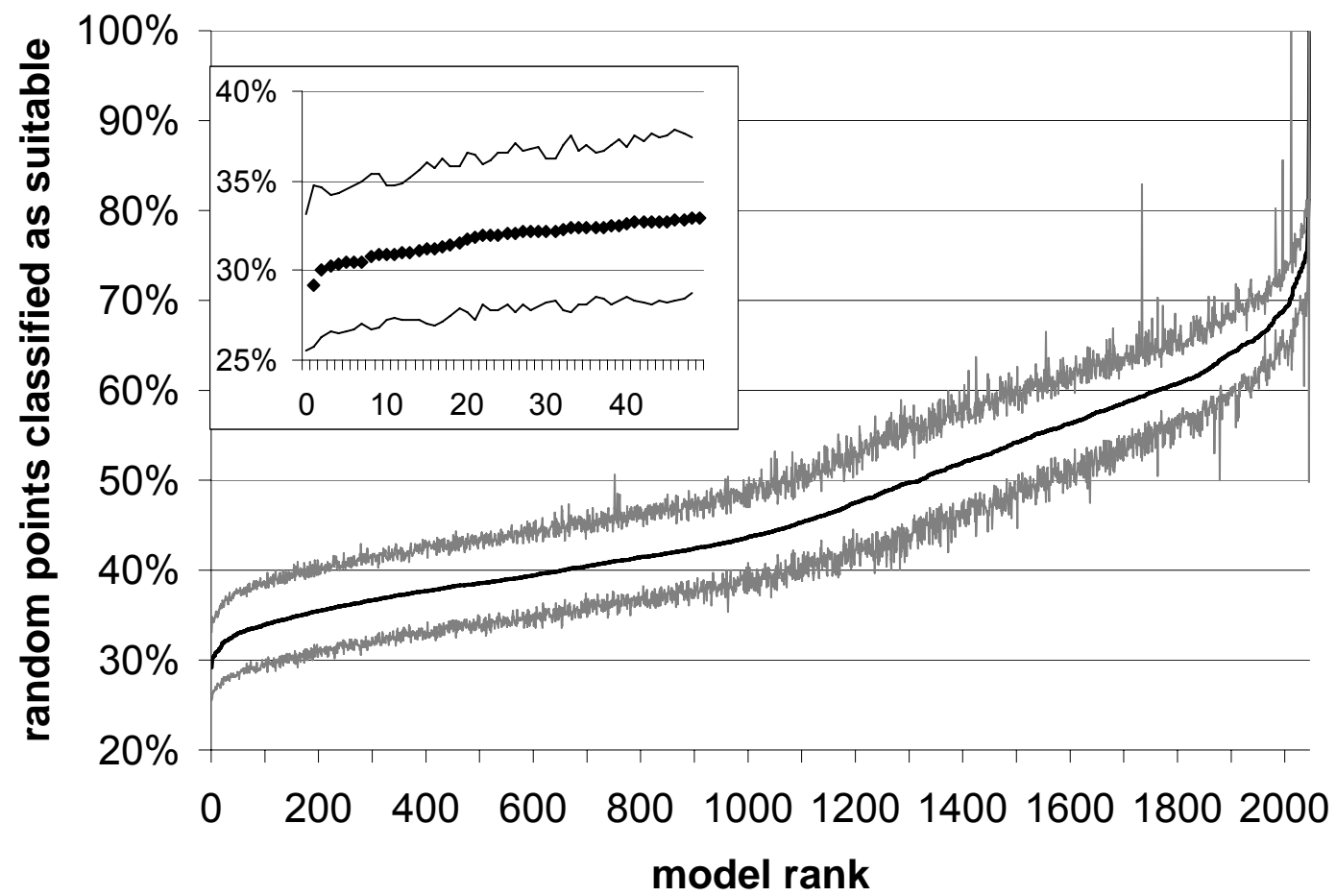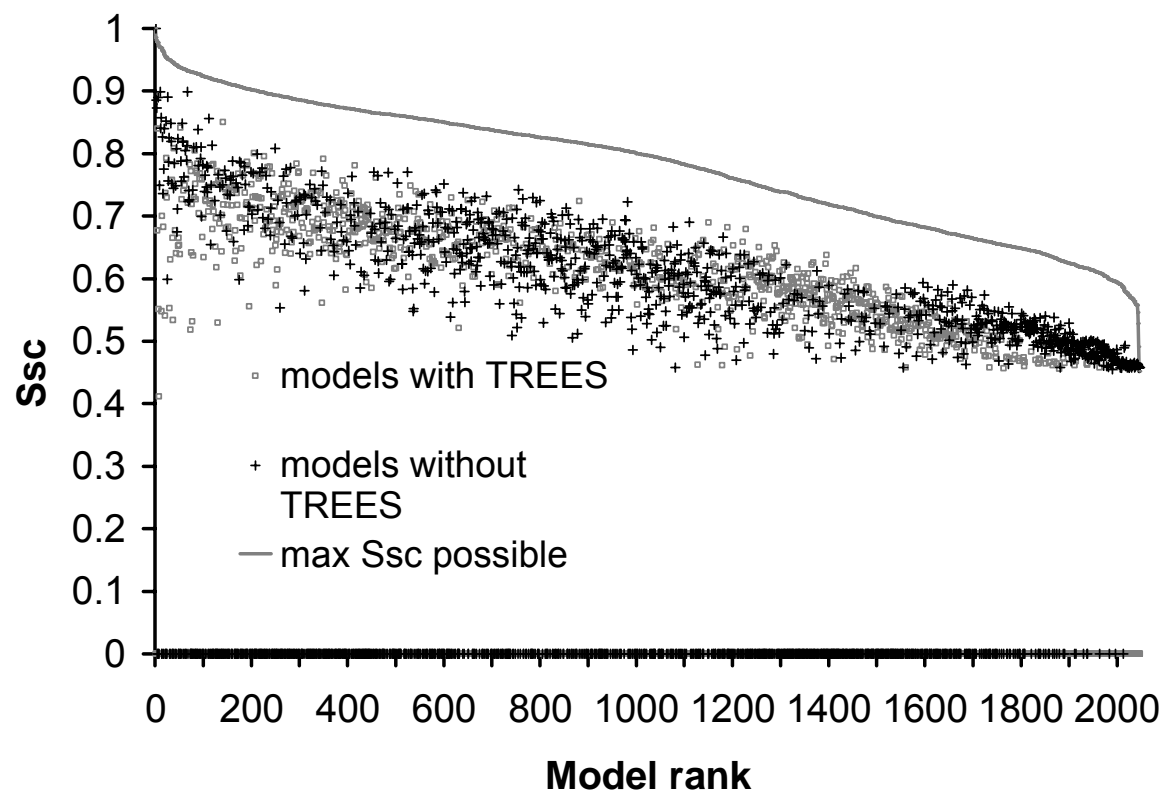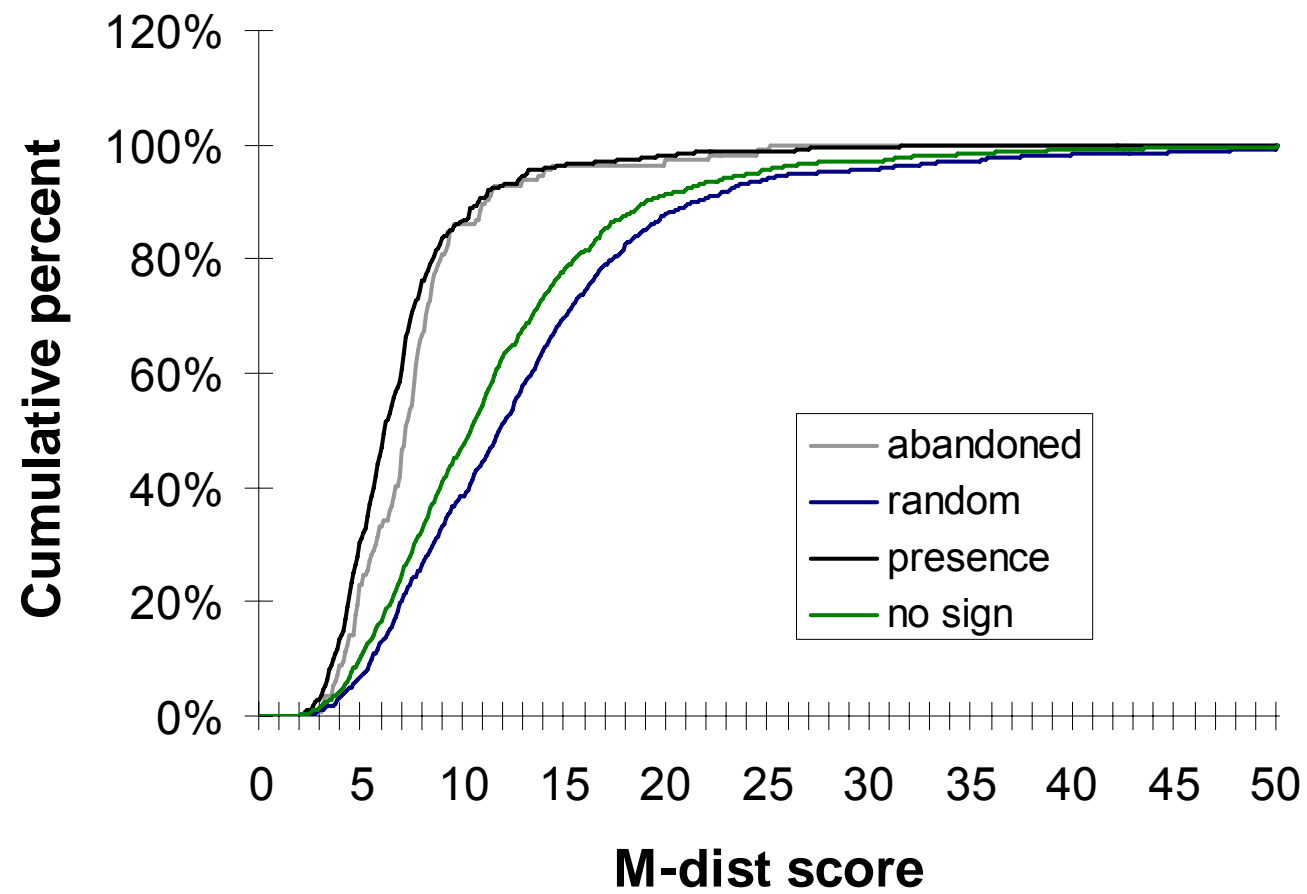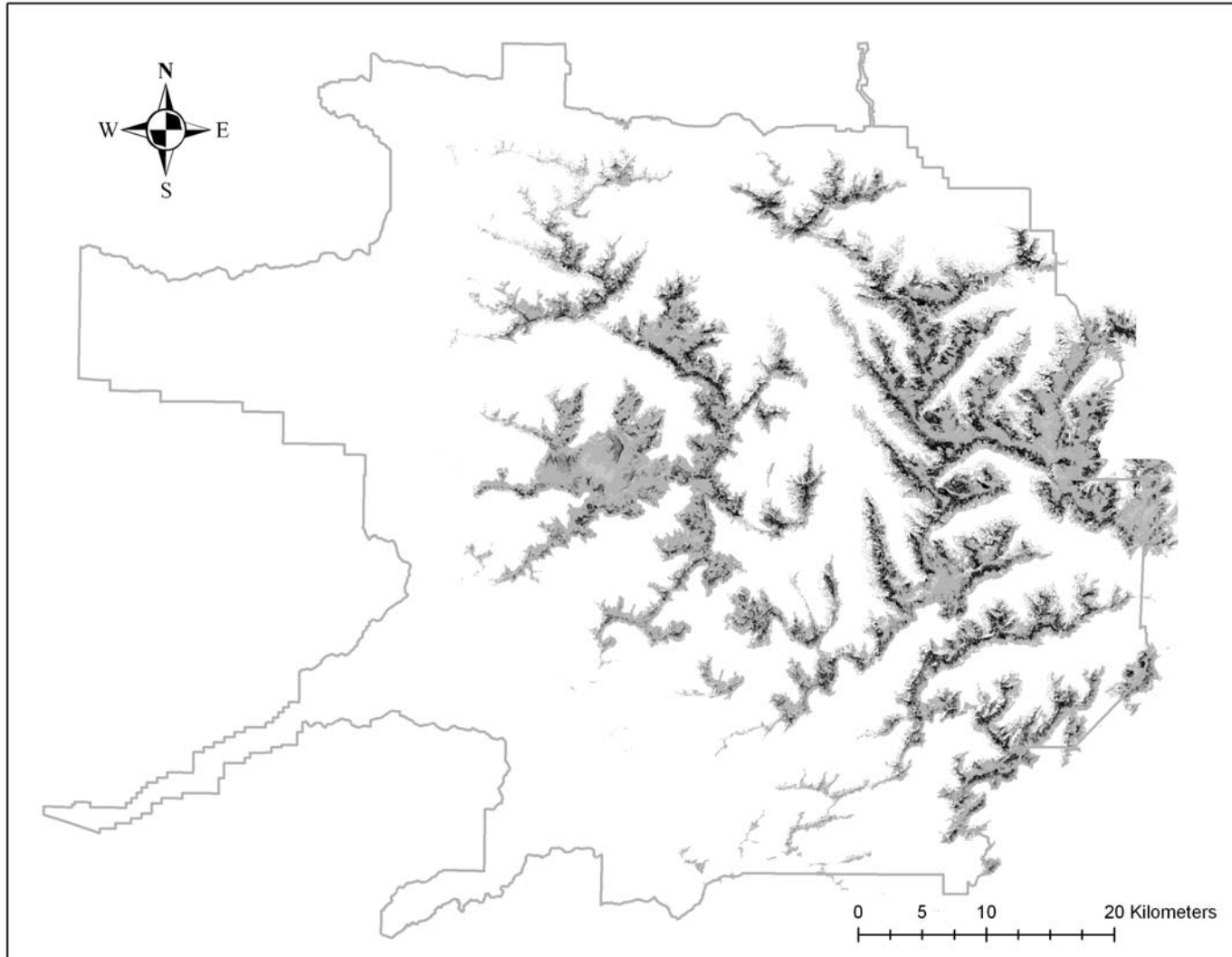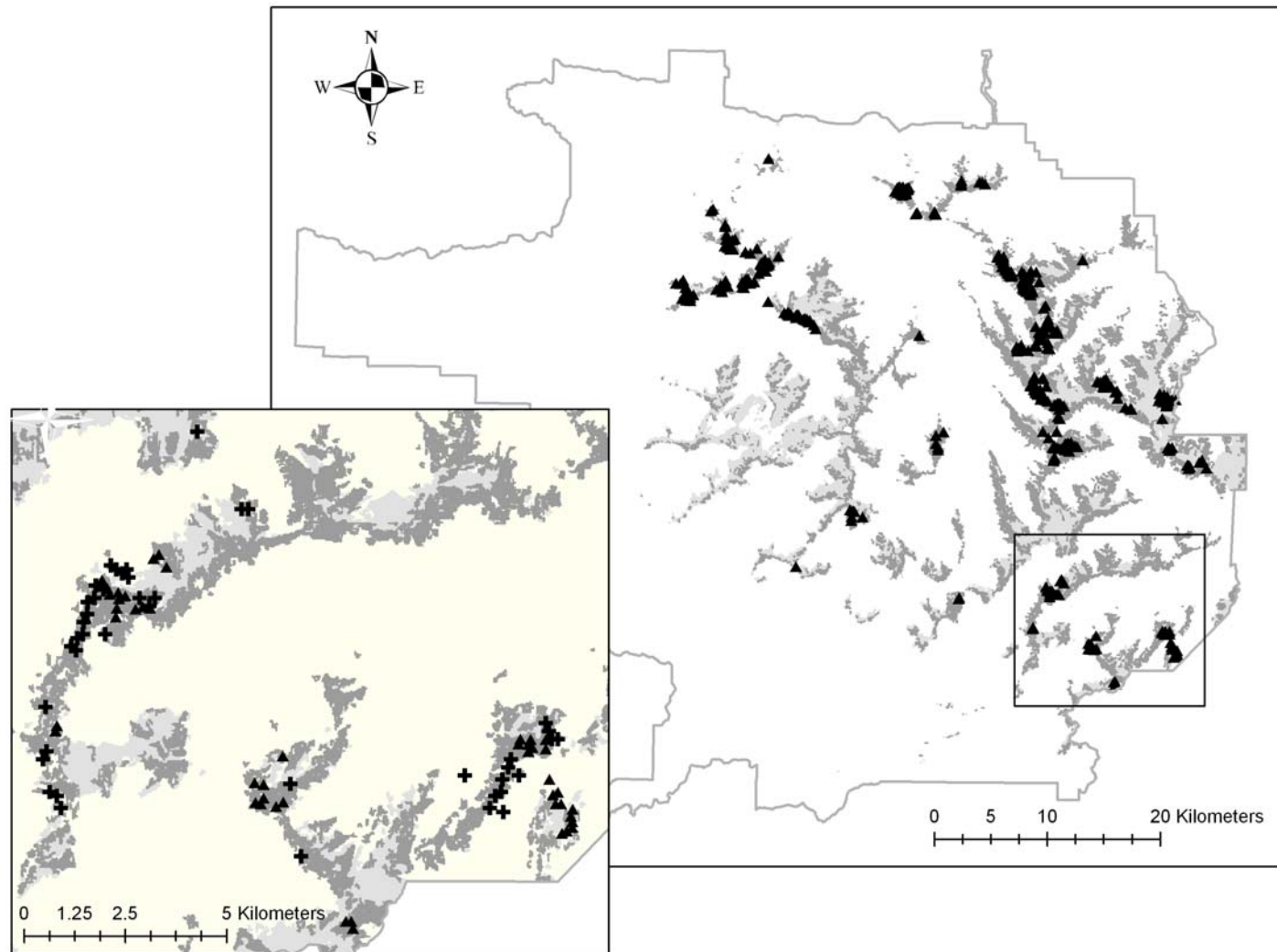
Appendices.

Appendix A. Olympic National Park snowpack trends
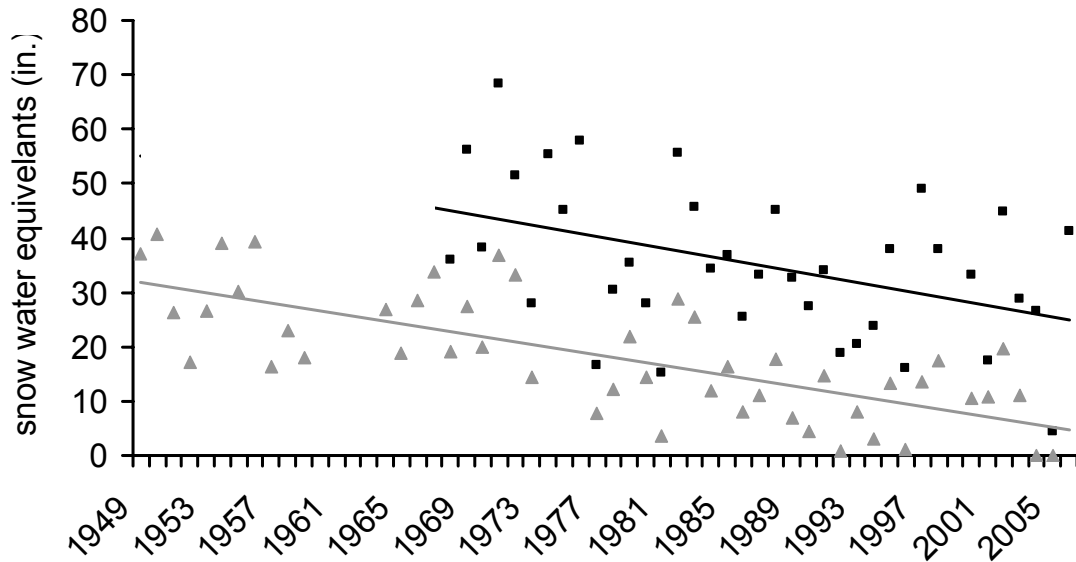
Figure A1. May 1 snow water equivalents (in inches) at Cox Valley (elevation 1385 m; black squares) and Deer Park (1600 m; gray triangles) in Olympic National Park (USDA Natural Resource Conservation Service 2006). Snow water equivalents, a measure of the amount of water in the snow-column, declined at Cox Valley by 0.53 inches year^{-1} over the period of record (least-squares linear regression, $P < 0.01$) and at Deer Park by 0.47 inches year^{-1} ($P<0.001$).

Appendix B. Olympic marmot home range estimates

Olympic marmot (*Marmota olympus*) home ranges in Olympic National Park. Data were collected on radio-tagged marmots during summers 2005 and 2006. Home ranges were calculated with Animal Movement Extension (Hooge & Eichenlaub 2000) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA).

Table B1. Home range estimates (100% minimum convex polygons) for individual marmots. Estimates for each individual are based on *n* active season locations from a single year (only a single location for each was recorded at the hibernaculum in the spring and fall). Three marmots were monitored for two years as indicated. Marmots for which two colony names are given dispersed during the summer of monitoring.

marmot	sex	age class	colony	*n*	area (ha)
Nao	f	adult	Eagle Point	37	0.66
Carolina	f	adult	Obstruction Point	35	6.22
Velocity (2005)	f	adult	Obstruction Point	30	3.39
Velocity (2006)	f	adult	Obstruction Point	40	4.85
Arnica	f	adult	Pumpkin Seed Lake	33	7.37
Phlox	f	adult	Pumpkin Seed Lake	40	13.24
CBS	f	adult	Hurricane Hill	51	6.26
Lightning	f	adult	Hurricane Hill	39	7.45
Matt's Marmot	f	adult	Hurricane Hill	37	8.09
Anastasia	f	adult	Royal Basin	28	0.51
Cleopatra	f	adult	Royal Basin	27	0.58
Elizabeth	f	adult	Royal Basin	26	0.72
Helen of Troy	f	adult	Royal Basin	31	0.80

marmot	sex	age class	colony	*n*	area (ha)
MQS	f	adult	Royal Basin	28	1.92
Nefertiti	f	adult	Royal Basin	29	0.66
Victoria	f	adult	Royal Basin	27	0.87
Mohawk	f	adult	Hurricane Hill	29	4.59
Pebbles	f	adult	Hurricane Hill	40	3.80
Tomo	m	adult	Eagle Point	36	0.82
Buddha	m	adult	Marmot Flats/ Pull-out	36	18.41
Tough Guy	m	adult	Marmot Flats	36	3.90
Carlo	m	adult	Obstruction Point	34	10.77
Fluffy	m	adult	Obstruction Point	23	12.61
Mergatroy (2005)	m	adult	Pumpkin Seed / Obstruction	36	20.67
Mergatroy (2006)	m	adult	Obstruction Point	34	15.72
Surf	m	adult	Pumpkin Seed Lake	36	12.09
Gwenivere	m	adult	Royal Basin	27	1.84
King Arthur	m	adult	Royal Basin	25	0.61
Labowsky	m	adult	Hurricane Hill	24	12.85
Rex	m	adult	Royal Basin	27	9.84
Victor	m	adult	Pull-out	28	2.56
Wingnut (2005)	m	adult	Cornus	27	12.06
Wingnut (2006)	m	adult	Cornus	42	20.28
Chance	f	subadult	Eagle Point	35	0.44
Falcon	f	subadult	Eagle Point	33	0.83
Hope	f	subadult	Eagle Point	22	3.01
Owl	f	subadult	Eagle Point	32	1.09
Hopper	f	subadult	Marmot Flats	36	4.83
Lillian	f	subadult	Marmot Flats	35	2.67
Arwen	f	subadult	Pumpkin Seed Lake	35	13.79

marmot	sex	age class	colony	*n*	area (ha)
Pippin	f	subadult	Pumpkin Seed Lake	35	8.03
Jupiter	f	subadult	Hurricane Hill	27	2.86
Kant	f	subadult	Hurricane Hill	40	73.74
Bonnie	f	subadult	Eagle Point / unmarked colony	43	13.21
Margarita	f	subadult	Pull-out	28	0.81
Muncaster	m	subadult	Marmot Flats	31	3.63
Prunus	m	subadult	Marmot Flats	36	5.06
Aristotle	m	subadult	Hurricane Hill	42	16.76
Squirrel	m	subadult	Hurricane Hill	41	5.24
Venus	m	subadult	Hurricane Hill	32	5.75

Table B2. Summary statistics for minimum convex polygon homerange estimates for Olympic marmots.

age / sex class	median (ha)	minimum (ha)	maximum (ha)	n
adult female	3.59	0.51	13.24	18
adult male	12.06	0.61	20.67	15
subadult	4.83	0.44	73.74	17
all marmots	4.84	0.44	73.74	50

Appendix C. Known-fate survival models

     We compared known-fate models in program Mark (White & Burnham 1999) to fit a suite of possible survival models to Olympic marmot (*Marmota olympus*) radio-telemetry data collected in Olympic National Park 2002-2006 (Table C1). There were three survival models for which $\Delta AIC_c \leq 2$, indicating that they had roughly equivalent support in the data. All three allowed adult female survival to vary across the season, while adult males and subadults shared a constant survival rate. These models differed only in how survival rates were assumed to vary among the site groups – the top ranked model provided for Royal Basin to have different survival rates from the other 2 site groups. Indeed, for all model structures, the model with a separate parameter for Royal Basin outranked the others. Royal Basin is geographically separate and topographically dissimilar from the other site groups. Perhaps because of these differences, marmot density is higher and reproductive performance is lower than at either the Western or Central sites, and it is therefore plausible that survival rates at Royal Basin could differ from the other site groups. Accordingly, we derived the survival estimates from this top-ranked model, which estimated annual survival of adult females to be considerably lower than that of adult males and subadults, and survival of all animals to be lower at the Western and Central site groups than at Royal Basin (Chapter 1, Table 2).

Table C1. Known-fate models compared in program MARK (White & Burnham 1999)

for survival analysis of Olympic marmot (*Marmota olympus*). Radio-telemetry data were

collected from 2002-2006 in Olympic National Park. ΔAIC_c (the difference in the

adjusted Akaike information criterion between each model and the top-ranked model), w_i

(the weight of evidence in favor of each model), and the number of parameters in each

model are shown. Bold font indicates the model used to derive survival rates.

Model	ΔAIC_c	w_i	No. of parameters
$t^{31}*AF^{32}+site2^{33}+winter$	**0.00**	**0.41**	**9**
t*AF+winter	1.21	0.22	8
t*AF+site3[34]+winter	1.94	0.15	10
t*class3[35,36]+site2+winter	3.64	0.07	21
June*AF[37]+sept[38]+site2+winter	4.59	0.04	4
t*class3+winter	5.27	0.03	20
June*AF+sept+winter	5.34	0.03	3
t*class3+site3+winter	5.60	0.02	22
June*AF+sept+site3+winter	6.50	0.02	5
class2[39]+winter	10.31	0.00	2
site2+winter	10.61	0.00	2
class3+winter	11.51	0.00	3
site3+winter	12.60	0.00	3
winter	12.65	0.00	2
t*class2[40]+site2+winter	13.77	0.00	18
t*class2+winter	14.91	0.00	17
t*class2+site3+winter	15.72	0.00	19
t+class2+winter	15.76	0.00	11
t+site2	15.88	0.00	11
t+class3+winter	17.25	0.00	12
t	17.82	0.00	11
t+site3	17.85	0.00	12

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[31] Sampling intervals were 10 0.5-month periods (May 1 – Sept. 30) and winter. t indicates that survival varied by interval, either for all animals or as indicated by interaction terms
[32] t*AF: survival of adult females varies by interval
[33] site2: Western and Central site groups differ from Royal Basin
[34] site3: Western, Central, and Royal Basin site groups all differ
[35] class3: adult females, adult males, and subadults all differ
[36] t*class3: survival varies by interval differently for adult females, adult males, and subadults
[37] June*AF: adult female survival differs only in June
[38] sept: survival of all animals differs in September from the rest of the active season
[39] class2: adult females differ from adult males and subadults
[40] t*class2: survival varies by interval differently for adult females and other animals

Appendix D. Mark-resight abundance models

We used program Mark (White & Burnham 1999) to fit a suite of possible models to Olympic marmot (*Marmota olympus*) mark-resight data collected in Olympic National Park 2002-2006. A different group of candidate models was fit to each of four sites or site groups (Tables 1-4; see methods for details about sites).

We analyzed the closed population portion of the resighting data with Huggins full heterogeneity models in program Mark (White & Burnham 1999). The Huggins models allow detection probability to vary among and within secondary sessions; initial capture probabilities ($p_{i,j}$, where *i* denotes the secondary session and *j* denotes the day within the secondary session) to differ from recapture probabilities ($c_{i,j}$); and a mixture of 2 groups with different capture probabilities. When 2 groups are modeled, there are 2 initial capture probabilities (p_a and p_b), and 2 recapture probabilities (c_a and c_b); the parameter π indicates the estimated proportion of the population in group a. The open population parameters in these models include: probability of survival between secondary sessions (S_i); the probability of an animal emigrating from the study area (g_i''); and the probability that an animal that left the study area remained off the study area (g_i'). The parameter of interest to us, estimated abundance $\hat{N}_i$ within each secondary session, is a derived parameter in Huggins models. We fit a slightly different suite of candidate models for each site group to account for differences in data structure and quantity.

At Royal Basin, the tall vegetation, steepness of the meadow, and the marmots' lack of habituation to humans led to relatively low and highly variable resighting probabilities, so we incorporated capture data into the models as an additional encounter session. Specifically, we trapped marmots at Royal Basin for 1-4 days within the week

proceeding each secondary session and combined this capture data into a single encounter session. Thus, each secondary session had 1 encounter session of captures and 3 encounter sessions of resightings. The capture encounter session in secondary session i was then modeled with a different detection parameter ($p_{i,trap}$) than that for the resightings within that session (hereafter collectively $p_{i,resight}$). We assumed that there was no behavioral response associated with being resighted and that there was no change in the probability of detection among resighting encounter sessions within a secondary sessions – that is $p_{i,resight} = c_i$ in all models. Candidate models included those in which the detection parameters were constant across all secondary sessions ($p_{.,resight} = c_.$), those in which resighting probabilities varied across all secondary session ($p_{t,resight} = c_t$), and those in which there were 2 detection parameters – 1 for the first 4 secondary sessions, when apparent marmot activity was high due to favorable weather, and 1 for the later secondary sessions, when extremely hot weather or rain resulted in little marmot activity and presumably lower detection probabilities ($p_{early\ v\ late,resight} = c_{early\ v\ late}$). Likewise, we included models in which capture (trapping) probabilities either varied across all secondary sessions ($p_{t,trap}$) or were constant ($p_{.,trap}$). No mixture parameter was included in the closed population portion of any models in the Royal Basin candidate set because it was unreasonable to expect that the mixture would be similar for resighting and trapping. In the open population portion of the models for Royal Basin, we included weekly survival as either a constant ($S_.$) or allowed it to vary across the 6 intervals (S_t). For all sites, we included models in which the movement rates were each estimated with a single parameter ($g''_.$ and $g'_.$) and those in which they were both set to 0 (g''_0 and g'_0). Our telemetry data indicate that emigration is too rare to estimate on a per interval basis. If the

probability g' is high, then *g''* can be set to 0 and dispersers will be modeled as if dead, with a resulting lower apparent survival estimate but no loss of information about $\hat{N}$.

At the Central site groups and Hurricane Hill, we did not necessarily trap immediately before resighting and so we did not incorporate this additional source of data in the closed population models. In the absence of that complication, we included in the candidate model sets for each site group models that allowed a mixture of detection probabilities within the population – that is, some portion of the animals were modeled as more detectable than others because they were generally more approachable, inhabited in less difficult terrain, or their eartags were cleaner. The parameter π_i denotes the proportion of the marmot populations with $p_{a,i}$, with 1- π_i denoting $p_{b,i}$. Therefore, when the mixture parameter is included in a model, the number of detection parameters that must be estimated is doubled. We ran models with π_1 (no mixture), $\pi_.$ (constant across intervals), and π_t (varying by interval) except at Central-B, where there was not enough data to estimate $\pi_.$ or π_t simultaneously with $p_{a,t}$ and $p_{a,t}$. A second difference at these site groups was that a high proportion of marmots were implanted with radio-transmitters for much of the study, providing reliable external data on survival patterns. Therefore, we fit models in which 1 survival parameter was estimated for intervals in which the telemetry data indicated generally high survival (intervals 2, 3, 4, and 5 at Hurricane Hill; 1, 3, 4, and 5 at Central-A; and 1, 3, and 6 at Central-B) and a 2nd survival parameter for those intervals with relatively lower survival, in addition to models with a $S_.$ and models with S_t.

We examined the model structure, estimates of $\hat{N}$, and associated 95% confidence intervals from all models with $\Delta AIC_c \leq 2$ for each site group to identify the

model from which we ultimately derived estimates of $\hat{N}$. If 2 models have the same structure but differ by the addition of 1 parameter, the more highly parameterized model would be expected to be within 2 AIC_c units of the less parameterized models even if the additional parameter contributes little or nothing to model fit (Burnham & Anderson 2002). In these cases, Burnham and Anderson recommend relying on the model with fewer parameters. We followed this suggestion, after examining the estimates of $\hat{N}$ from these models with comparable support.

Table D1. Models compared in program Mark to estimate abundance of Olympic marmots at four sites or site groups in Olympic National Park, Washington, USA. See text for a description of the parameters estimated. ΔAIC_c (the difference in the adjusted information criterion between each model and the top-ranked model), w_i (the weight of evidence in favor of each model), and the number of parameters in each model are shown. The models used to derive $\hat{N}$ are indicated with bold font.

Model	ΔAIC_c	(w_i)	No. of parameters
Royal Basin			
$S_.$ g''_0 g'_0 $p_{t,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	**0.00**	**0.59**	**9**
$S_.$ $g''_.$ $g'_.$ $p_{t,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	2.14	0.20	10
$S_.$ g''_0 g'_0 $p_{t,trap}$ $p_{resight} = c_t$	3.36	0.11	14
$S_.$ $g''_.$ $g'_.$ $p_{t,trap}$ $p_{resight} = c_t$	5.08	0.05	16
S_t g''_0 g'_0 $p_{t,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	5.62	0.04	14
S_t $g''_.$ $g'_.$ $p_{t,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	9.29	0.01	16
S_t g''_0 g'_0 $p_{t,trap}$ $p_{resight} = c_t$	9.50	0.01	19
S_t $g''_.$ $g'_.$ $p_{t,trap}$ $p_{resight} = c_t$	11.70	0.00	21
$S_.$ g''_0 g'_0 $p_{.,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	24.01	0.00	4
$S_.$ $g''_.$ $g'_.$ $p_{.,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	26.08	0.00	5
S_t g''_0 g'_0 $p_{.,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	30.59	0.00	9

Model	Δ	w	K
$S._.$ $g''._.$ $g'._.$ $p_{.,trap}$ $p_{.,resight} = c._.$	32.13	0.00	5
$S._.$ g''_0 g'_0 $p_{.,trap}$ $p_{.,resight} = c._.$	32.29	0.00	3
S_t $g''._.$ $g'._.$ $p_{.,trap}$ $p_{early\ v\ late,resight} = c_{early\ v\ late}$	32.73	0.00	10
S_t g''_0 g'_0 $p_{.,trap}$ $p_{.,resight} = c._.$	38.41	0.00	8
S_t $g''._.$ $g'._.$ $p_{.,trap}$ $p_{.,resight} = c._.$	38.58	0.00	10
Central-A			
S_{2rates} g''_0 g'_0 π_t $p._.=c._.$	**0.00**	**0.70**	**14**
S_{2rates} $g''._.$ $g'._.$ π_t $p._.=c._.$	2.13	0.24	15
S_{2rates} g''_0 g'_0 π_1 $p_t=c_t$	6.72	0.02	12
$S._.$ g''_0 g'_0 π_t $p._.=c._.$	7.08	0.02	13
$S._.$ $g''._.$ $g'._.$ π_t $p._.=c._.$	9.20	0.01	14
S_{2rates} $g''._.$ $g'._.$ π_1 $p_t=c_t$	9.89	0.00	14
S_t g''_0 g'_0 π_t $p._.=c._.$	10.36	0.00	21
S_t $g''._.$ $g'._.$ π_t $p._.=c._.$	12.55	0.00	22
S_{2rates} g''_0 g'_0 $\pi._.$ $p._.=c._.$	12.85	0.00	5
$S._.$ g''_0 g'_0 π_1 $p_t=c_t$	14.47	0.00	11
S_{2rates} g''_0 g'_0 $\pi._.$ $p_t=c_t$	14.82	0.00	23
S_{2rates} $g''._.$ $g'._.$ $\pi._.$ $p._.=c._.$	16.49	0.00	7
S_t g''_0 g'_0 π_1 $p_t=c_t$	16.54	0.00	19
$S._.$ $g''._.$ $g'._.$ π_1 $p_t=c_t$	17.43	0.00	13
$S._.$ g''_0 g'_0 $\pi._.$ $p._.=c._.$	18.12	0.00	4
S_t $g''._.$ $g'._.$ π_1 $p_t=c_t$	18.71	0.00	20
S_{2rates} $g''._.$ $g'._.$ $\pi._.$ $p_t=c_t$	19.18	0.00	25
$S._.$ $g''._.$ $g'._.$ $\pi._.$ $p._.=c._.$	20.16	0.00	5
$S._.$ g''_0 g'_0 $\pi._.$ $p_t=c_t$	21.07	0.00	22
S_{2rates} $g''._.$ $g'._.$ π_1 $p._.=c._.$	21.09	0.00	5
S_t g''_0 g'_0 $\pi._.$ $p._.=c._.$	22.69	0.00	12
$S._.$ $g''._.$ $g'._.$ $\pi._.$ $p_t=c_t$	23.34	0.00	23
S_t g''_0 g'_0 $\pi._.$ $p_t=c_t$	23.98	0.00	29
S_t $g''._.$ $g'._.$ $\pi._.$ $p._.=c._.$	24.80	0.00	13
S_{2rates} g''_0 g'_0 π_t $p_t=c_t$	25.87	0.00	29
S_t $g''._.$ $g'._.$ $\pi._.$ $p_t=c_t$	26.35	0.00	30
$S._.$ $g''._.$ $g'._.$ π_1 $p._.=c._.$	26.53	0.00	4
S_{2rates} $g''._.$ $g'._.$ π_t $p_t=c_t$	28.13	0.00	30
S_{2rates} g''_0 g'_0 π_1 $p._.=c._.$	28.27	0.00	3
$S._.$ g''_0 g'_0 π_t $p_t=c_t$	29.78	0.00	27

Model	ΔAIC	w	K
$S_t\ g''.\ g'.\ \pi_1\ p.=c.$	30.95	0.00	12
$S.\ g''_0\ g'_0\ \pi_1\ p.=c.$	33.22	0.00	2
$S_t\ g''_0\ g'_0\ \pi_t\ p_t=c_t$	33.56	0.00	34
$S.\ g''.\ g'.\ \pi_t\ p_t=c_t$	36.47	0.00	30
$S_t\ g''_0\ g'_0\ \pi_1\ p.=c.$	36.93	0.00	10
$S_t\ g''.\ g'.\ \pi_t\ p_t=c_t$	45.10	0.00	39

Central-B

Model	ΔAIC	w	K
$S.\ g''.\ g'.\ \pi_1\ p.=c.$	**0.00**	**0.38**	**4**
$S_{2rates}\ g''.\ g'.\ \pi_1\ p.=c.$	1.99	0.14	5
$S.g''.\ g'.\ \pi.\ p.=c.$	2.15	0.13	5
$S.\ g''_0\ g'_0\ \pi.\ p.=c.$	2.93	0.09	4
$S_{2rates}\ g''.\ g'.\ \pi.\ p.=c.$	4.18	0.05	6
$S.\ g''_0\ g'_0\ \pi_1\ p_t=c_t$	4.71	0.04	8
$S_{2rates}\ g''_0\ g'_0\ \pi.\ p.=c.$	4.78	0.04	5
$S.\ g''_0\ g'_0\ \pi_1\ p.=c.$	5.02	0.03	2
$S.\ g''_0\ g'_0\ \pi_t\ p.=c.$	5.95	0.02	10
$S_t\ g''.\ g'.\ \pi_1\ p.=c.$	6.06	0.02	9
$S.g''.\ g'.\ \pi_1\ p_t=c_t$	6.49	0.01	10
$S_{2rates}\ g''_0\ g'_0\ \pi_1\ p_t=c_t$	6.80	0.01	9
$S_{2rates}\ g''_0\ g'_0\ \pi_1\ p.=c.$	6.81	0.01	3
$S_{2rates}\ g''_0\ g'_0\ \pi_t\ p.=c.$	8.20	0.01	11
$S_t\ g''.\ g'.\ \pi.\ p.=c.$	8.38	0.01	10
$S_t\ g''_0\ g'_0\ \pi.\ p.=c.$	8.58	0.01	9
$S_{2rates}\ g''.\ g'.\ \pi_1\ p_t=c_t$	8.74	0.00	11
$S_t\ g''_0\ g'_0\ \pi_1\ p.=c.$	10.12	0.00	7
$S.\ g''.\ g'.\ \pi_t\ p.=c.$	10.83	0.00	12
$S_t\ g''_0\ g'_0\ \pi_1\ p_t=c_t$	10.98	0.00	13
$S_t\ g''_0\ g'_0\ \pi_t\ p.=c.$	13.08	0.00	15
$S_{2rates}\ g''.\ g'.\ \pi_t\ p.=c.$	13.18	0.00	13
$S_t\ g''.\ g'.\ \pi_1\ p_t=c_t$	13.60	0.00	15
$S_t\ g''.\ g'.\ \pi_t\ p.=c.$	18.44	0.00	17

Hurricane Hill

Model	ΔAIC	w	K
$S_{2rates}\ g''.\ g'.\ \pi_1\ p_t=c_t$	0.00	0.37	13
$S.\ g''.\ g'.\ \pi_1\ p_t=c_t$	**0.11**	**0.35**	**12**
$S.g''.\ g'.\ \pi_1\ p.=c.$	3.55	0.06	4
$S_{2rates}\ g''.\ g'.\ \pi_1\ p.=c.$	3.69	0.06	5

Model			
S_{2rates} g" g' π. p.=c.	3.98	0.05	7
S.g" g' π_t p.=c.	4.11	0.05	14
S.g" g' π. p.=c.	4.18	0.05	6
S_{2rates} g" g' π_t p.=c.	7.07	0.01	15
S_t g" g' π_1 $p_t=c_t$	9.29	0.00	19
S. g"$_0$ g'$_0$ π_1 p.=c.	10.10	0.00	3
S_{2rates} g"$_0$ g'$_0$ π_1 p.=c.	10.19	0.00	4
S(t g" g' π_1 p.=c.	10.65	0.00	10
S. g"$_0$ g'$_0$ π. p.=c.	10.77	0.00	5
S_{2rates} g"$_0$ g'$_0$ π. p.=c.	10.80	0.00	6
S_t g" g' π. p.=c.	13.86	0.00	13
S_t g" g' π_t p.=c.	13.87	0.00	21
S_{2rates} g" g' π. $p_t=c_t$	16.38	0.00	23
S.g" g' π. $p_t=c_t$	16.62	0.00	22
S_{2rates} g"$_0$ g'$_0$ π_t p.=c.	24.30	0.00	13
S. g"$_0$ g'$_0$ π_t p.=c.	24.70	0.00	12
S_t g"$_0$ g'$_0$ π. p.=c.	25.05	0.00	11
S_{2rates} g" g' π_t $p_t=c_t$	27.51	0.00	28
S_t g" g' π. $p_t=c_t$	29.35	0.00	29
S.g" g' π_t $p_t=c_t$	30.55	0.00	28
S_{2rates} g"$_0$ g'$_0$ π. $p_t=c_t$	31.95	0.00	21
S_{2rates} g"$_0$ g'$_0$ π_1 $p_t=c_t$	36.01	0.00	11
S. g"$_0$ g'$_0$ π. $p_t=c_t$	36.31	0.00	20
S. g"$_0$ g'$_0$ π_1 $p_t=c_t$	38.01	0.00	10
S_t g" g' π_t $p_t=c_t$	39.56	0.00	34
S_t g"$_0$ g'$_0$ π_1 p.=c.	42.76	0.00	8
S. g"$_0$ g'$_0$ π_t $p_t=c_t$	44.46	0.00	26
S_t g"$_0$ g'$_0$ π_t p.=c.	44.86	0.00	19
S_t g"$_0$ g'$_0$ π_1 $p_t=c_t$	44.90	0.00	17
S_t g"$_0$ g'$_0$ π. $p_t=c_t$	46.54	0.00	27
S_{2rates} g"$_0$ g'$_0$ π_t $p_t=c_t$	50.48	0.00	26
S_t g"$_0$ g'$_0$ π_t $p_t=c_t$	58.75	0.00	31

Appendix E. Cause of death for radio-tagged Olympic marmots.

Table E1. Assigned cause of death and evidence supporting that assignment for 43 radio-tagged Olympic marmots 2002-2006.

Case	Year	Name	Site group	Age	Sex	Assigned cause	Evidence
1	2002	Vagabond	Western	2	f	coyote	intact carcass cached in dug hole; post-mortem indicated rib-cage crushed by canine jaws
2	2002	Salem	Western	1	f	coyote	killing witnessed; intact carcass cached
3	2002	Rocky	Western	A	m	coyote	intact carcass cached; puncture wounds in head
4	2002	Jabba	Western	A	m	predation	transmitter near burrow under snow in spring
5	2002	Evening Star	Central	A	f	predation	transmitter found in open in spring
6	2002	Debbie	Western	A	f	coyote	killing witnessed
7	2003	Granite	Western	A	f	lost	
8	2003	Toothless	Western	A	m	predation	transmitter found in tree well
9	2003	Johanna	Central	A	f	lost	female; bred previous year
10	2003	Olive Oil	Central	A	f	predation	transmitter found

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11	2004	San	Western	A	f	predation	transmitter found in forest
12	2004	Tanya	Western	A	f	in burrow	transmitter under large rock, not recovered
13	2004	Beatrice	Royal	A	f	lost	female with young-of-the-year
14	2004	Lily	Central	A	f	in burrow	transmitter in burrow, not recovered
15	2004	Abies	Central	1	f	carnivore	transmitter and gut pile recovered
16	2004	Mara	Central	A	f	predation	transmitter and a few hairs found
17	2004	Heather	Central	A	f	lost	female with young-of-the-year
18	2005	Miwa	Central	A	f	lost	female; bred previous two years
19	2005	Artemis	Royal	A	f	coyote	hindquarters cached in dug hole
20	2005	Beanbag	Central	A	f	lost	female with yearlings and 2-year-olds
21	2005	Rainbow	Central	A	f	lost	
22	2005	Dede	Western	A	f	coyote	coyote toothmarks in transmitter
23	2005	Prince William	Royal	A	m	lost	
24	2005	Leonard	Central	A	m	coyote	toothmarks in transmitter consistent with coyote
25	2005	Lena	Central	A	f	carnivore	toothmarks from unidentified carnivore

26	2005	Mouse	Western	1	f	raptor	frresh carcass with plucked fur and feathers
27	2005	Lucky	Central	1	f	carnivore	gut pile under very dense saplings
28	2005	Ramses	Royal	A	m	eagle	entire marmot recovered from burrow; post-mortem revealed puncture wounds consistent with eagle
29	2005	Carlo	Central	A	m	lost	disappeared in late-September
30	2005	Carrie	Central	1	f	lost	disappeared in late-September
31	2006	Labowsky	Western	A	m	eagle	whitewash and feathers at carcass; plucked fur and gut pile
32	2006	Big Al	Western	A	m	predation	
33	2006	Ghengis Khan	Royal	A	m	coyote	toothmarks in transmitter consistent with coyote
34	2006	Lupine	Central	A	m	coyote	toothmarks in transmitter consistent with coyote
35	2006	Picea	Central	A	m	coyote	toothmarks in transmitter consistent with coyote
36	2006	Socrates	Western	2	m	eagle	eagle tracks in snow; plucked fur, blood, and gut pile
37	2006	Victor	Central	A	m	coyote	hindquarters, feet and part of skull recovered from tree well on open slope

38	2006	Vole	Western	2	m	cougar	disperser, carcass recovered in mid-elevation forest; organ consumed; remainder cached; cougar tracks and scat nearby
39	2006	CBS	Western	A	f	in burrow	transmitter in burrow; transmitter and some fur expelled from burrow several weeks later
40	2006	Hestor	Central	A	f	coyote	toothmarks in transmitter consistent with coyote; feet and gut pile found in tree clump
41	2006	Margot	Royal	A	f	lost	female with yearlings
42	2006	Hope	Central	2	f	carnivore	gut pile and various body parts cached in forest
43	2006	Fluffy	Central	A	m	carnivore	gut pile under very dense saplings

Appendix F. Matlab code for Mahalanobis distance habitat modeling presented in Chapter 5. All functions are .m files.

F1. Functions used to compute P_{r80} for 2500 bootstrapped samples of the 376 occupied points described in the text.

- variables.m
    - Inputs
        - *habitat*: a row vector of the habitat covariate names; in the case described in the text, *habitat* was 1 row by 11 columns.
    - Outputs
        - *Models*: a matrix of 0's and 1's for the models under consideration, where 1's indicate the column numbers of the variables to include in a given model and 0's indicate which to omit. This matrix is created with the function variables.m. In the case described in th e text, 11 habitat covariates resulted in a matrix of 2047 rows and 11 columns.
- BootstrapTopMdist.m
    - Inputs:
        - *Presentall*: a matrix of habitat covariate values for all occupied locations. The data set described in the text contained 376 rows and 11 columns.
        - *Random*: a matrix of habitat covariate values for all random locations. The data set described in the text contained 1000 rows and 11 columns.

- ▪ *Models*: output from variables.m

- ▪ *T:* is the threshold proportions at which we wish to compute the specificity. These specificities are equivalent to P_{rX} * 100; that is, enter 85, not 0.85. In the example in the text, the T was [85].

  - o Output

    - ▪ bootstrapresults2047_2500.txt is a matrix of P_{rX} values with each row representing a single bootstrap replicate and each column representing a single model.

Note that this output matrix is too large to import into Excel. Statistics of interest, such as the mean, variance, and confidence intervals for each model, need to be computed in Matlab before importing into Excel.

- • mdist.m is a subroutine needed to run BootstrapTopMdist.m although it can be used alone to compute Mahalanobis distance scores for any set of cases based on the distribution of any other set of cases. This file computes the Mahalanobis distance values for each row of both matrices based on the means and v-cv matrix from P, and outputs these distances in two vectors, p & r, corresponding to P & R.

  - o Inputs:

    - ▪ P: the "training data" – a matrix of n rows by v columns where each row holds the values of the v habitat variables for the particular case. Created in BootstrapTopMdist.m

    - ▪ R: the corresponding matrix of habitat values for random locations

  - o Outputs:

    - ▪ p: vector of mdist scores for training data

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- r: vector of mdist scores for random points

- discrim.m a subroutine needed to run BootstrapTopMdist.m . It computes the values of P_{rX} as described in the text with X representing the proportion of occupied locations to be correctly classified.

    o Inputs

        - p: vector of mdist scores for training data

        - r: vector of mdist scores for random points

        - T: described above although if this function is used outside the BootstrapTopMdist.m function, T can be a vector.

    o Output

        - d is a vector of the P_{rX}'s.

% **Function: variables.m**

% variables creates a matrix of all possible combinations of 0's and 1's
% for a given number of variables (length [i.e., number of columns] of
% *habitat*). Output is a matrix size (2^c,c) where c is the number of columns
% (variables) in input matrix *habitat* and 2^c is the number of possible
% combinations of these variables*.*

```
function models=variables(habitat)
    c=length(habitat);                 % determine number of columns in habitat
    models=zeros(2^c,c);               % create a matrix of zeros to hold results

   for i=1:2^c                         % 0's and 1's are assigned inside loop.
      for j=1:c
         if rem(round(i/(2^(j-1))),2)==1;
            models(i,j)=1;
         end
      end
   end
   models(2^c,:)=[ ];                  % deletes the last row since it is all zeros and so
                                       % does not represent a useable model.
```

%**Function: BootstrapTopMdist.m**
% *presentall*: matrix of habitat covariate values for all presence points
% *random*: matrix of habitat covariate values for random points
% *models*: a matrix of 0's and 1's for the models under consideration, where 1's indicate
%   the column numbers of the variables to include in a given model and 0's indicate
%   which to omit.
% *T*: a vector of threshold proportions at which we wish to compute the
%   specificity. These specificities are equivalent to P_{rx} * 100; that is, enter 85, not 0.85.

% this function takes the top set of models, whatever the number of models of interest
% is, computes the specificity (P_{rx}) at the threshold level *T*, for *reps* bootstrap
% replicates of each model. The training data is bootstrapped (with
% replacement) from *presentall*.

```
function output=BootstrapTopMdist(presentall, random, models, T)

%*****************************************************************************

% ENTER reps AS APPROPRIATE

reps=2500;                              %  number of bootstrap replicates
bs=376                                  %  sample size for each bootstrap

%*****************************************************************************

nm=size(models,1);                      %  number of models in models set
nv=size(models,2);                      %  number of variables in dataset

output=zeros(reps, nm);

for i=1:reps
    sample=zeros(bs,nv);                %  create empty matrix "sample" for bootstrapped
                                        %  presence data
    x=round((rand(bs,1)*(bs-1))+1);     %  select random integers between 1 and bs

    for k=1:bs
        sample(k,:)=presentall(x(k,1),:); %  fill in matrix sample with bootstrap sample
    end

    for j=1:nm
        v=find(models(j,:));            %  identify the columns (variables) to use in this loop
        P=sample(:,v);                  %  select the appropriate columns of the presence data
        R=random(:,v);                  %  select the appropriate columns of the random data
        [p,r]=mdist(P,R);               %  run the mdist program to get two vectors of scores
        d=discrim(p,r,T);               %  run the function that determines P_rx at percentiles T
        output(i,j)=d;                  %  put d [which is the P_rx] into the output matrix
    end
end
dlmwrite('bootstrapresults2047_2500', output, 'delimiter', '\t', 'precision', 15)
```

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% **Function: mdist.m**
% P: the "training data" – a matrix of n rows by v columns where each row holds
%   the values of the v habitat variables for the particular case.
% R: the corresponding matrix of habitat values for random locations
% This filed computes the Mahalanobis distance values for each row of
% both matrices based on the means and v-cv matrix from P, and outputs these
% distances in two vectors, p & r, corresponding to P & R.

function[p,r]=mdist(P,R)

%**

% ENTER sp AND sr AS APPROPRIATE

sp=376;   % number of rows (cases) in P
sr=1000;   % number of rows (cases) in R

%**

mu=mean(P);   % compute the mean of each habitat variable in P
sigma=cov(P);   % compute the inverse variance-covariance of P
inverse=inv(sigma);

MU1 = repmat(mu,[sp 1]);   % subtract the mean from all cases
Diff=P-MU1;
DT=Diff';   % transpose the resulting difference matrix

for i=1:sp   % compute the Mdist scores for all cases of P
   p(i,1)=Diff(i,:)*inverse*DT(:,i);
end

MU2 = repmat(mu,[sr 1]);   % repeat for R
Diff=R-MU2;
DT=Diff';

for i=1:sr
   r(i,1)=Diff(i,:)*inverse*DT(:,i);
end

% **Function: discrim.m**
% This function computes the values of P_{rX} as described in the text with X representing
%   the proportion of occupied locations to be correctly classified.
% p: vector of mdist scores for training data
% r: vector of mdist scores for random points
% T: a vector of threshold proportions at which we wish to compute the
% specificity. These specificities are equivalent to P_{rX}*100 (i.e., for 0.85 enter 85)
% Output, d, is a vector of the P_{rX}'s.

```
function d=discrim(p,r,T)

psort=sort(p);                 %  sort p and r each from smallest to biggest
rsort=sort(r);

d=zeros(length(T),1);          %  create a vector length T to hold the results

for i=1:length (p)             %  compute the percentile of each case of p
   s(i,1)=i/length(p);
end


%  this section finds the highest mdist score in p that is below the
%  T(j)percentile and then identifies the percentile of the r vector
%  corresponding to that that value and puts that percentile into vector d.
%  Repeats for each value in T.

for j=1:length(T)
   dd=max(find(s<T(j)));
   md=psort(dd);
   d(j)=T(j)-(max(find(rsort<=md)))/length(r);
end
```

F2. Functions used to compute the Sorrensen's similarity coefficient between the top

ranked and each of the other 2046 potential habitat models.

- **Ssc_allmodels** requires the submodel mdist.m described in D1

  - Inputs

    - *Presence*: same as *presenceall* described in D1

    - *Random*: same as described in D1

    - *Models***:** same as described in D1

    - *T***:** same as described in D1

  - Outputs

    - Ssc2047.txt is a the Ssc values appended to the *models* input

      matrix as final column.

```
%  Function: Ssc_allmodels
%  outputs a matrix (Ssc) of the Sorrensen similarity coeffiecients (appended
%  to the for the end of the models matrix).
%  assignment of random points as suitable or non-suitable habitat based on
%  each of the Mahalanobis distance models under consideration as compared
%  with the top ranked model.

%  Presence: a matrix of habitat covariate values for all occupied locations. The data set
%    described in the text contained 376 rows and 11 columns.
%  Random: a matrix of habitat covariate values for all random locations. The data set
%    described in the text contained 1000 rows and 11 columns.
%  models: a matrix of 0's and 1's for the models under consideration, where 1's indicate
%    the column numbers of the variables to include in a given model and 0's indicate
%    which to omit.
%  T: a vector of threshold proportions at which we wish to compute the
%    specificity. These specificities are equivalent to $P_{rx}$ * 100; that is, enter 85, not 0.85.

%  Each row of Ssc will represent the results from 1 model compared with the
%  previously defined best model. In the end, the Ssc values are appended to
%  the models matrix so the Ssc values are linked to the corresponding model.

function results = Ssc_allmodels (presence, random, models, T)

V=models;
Ssc=zeros(length(V),1);
x=(round(T*size(presence,1)));
```

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```
mapA=zeros(length(random),1);

%  the following sequence determines if each random location is (1) or is not (0) suitable
%  habitat according to the top-ranked model.

v=find(V(1,:));                    %  identify the columns (variables) to use this loop
P=presence(:,v);                   %  select the appropriate columns of the presence data
R=random(:,v);                     %  select the appropriate columns of the random data
[p,r]=mdist(P,R);                  %  run the mdist program to get two vectors of scores
psort=sort(p);                     %  sorts the Mdist scores for the presence data
cut=psort(x);                      %  identifies the Mdist value that represents T percentile
for i=1:length(r)                  %  assigns each random value to being suitable (1) or
   if r(i)>cut                     %  unsuitable (0) based on the top ranked model.
      mapA(i)=0;
   else
      mapA(i)=1;
   end
end

%  for each possible model, as identified in V and indexed to v, compute the
%  M-dist for training and random data, then compute the discrimination at
%  each of the desired percentiles, then add results to the appropriate row
%  of vector Ssc.

for i=1:length(V);                 %  for each possible model (i.e, all models in V)
   v=find(V(i,:));                 %  identify the columns (variables) to use this loop
   P=presence(:,v);               %  select the appropriate columns of the presence data
   R=random(:,v);                 %  select the appropriate columns of the random data
   [p,r]=mdist(P,R);              %  run the mdist program to get two vectors of scores
   mapB=zeros(length(r),1);
   for k=1:length(r)              %  assigns each random value to being suitable (1) or
      if r(k)>cut                 %  unsuitable (0) based on the top ranked model.
         mapB(k)=0;
      else
         mapB(k)=1;
      end
   end
   a=0;
   b=0;
   c=0;
   for j=1:length(mapB)
      if (mapB(j)+ mapA(j))==2;
         b=b+1;
      elseif mapB(j)< mapA(j);
         a=a+1;
      elseif mapB(j)>mapA(j);
         c=c+1;
      end;
   end
   i=i
   s(i,1) =((2*b)/(a+(2*b)+c));          %  compute Ssc for row i of matrix Ssc
```

```
end

results=[V s];

dlmwrite('Ssc2047.txt', results, 'delimiter', '\t', 'precision', 15)
```

Appendix G. Summary of genetic samples collected and primer screening

Introduction

From 2001-2006, hair samples were collected from Olympic marmots throughout Olympic National Park for genetic analysis of spatial structure ($n = 414$ samples, of which some may be duplicates), tissue or hair samples were taken from ~200 tagged marmots for kinship analysis, and hair samples ($n = 314$; representing ~70 individuals) were collected in a mark-recapture framework at six sites to monitor abundance over time. Some of the samples from the later two groups could be incorporated into any analysis of spatial structure as well.

Polymorphic primers were identified and most samples were extracted and amplified at least once. As the data set is not complete, analyses are not included herein but the field and lab methods are summarized.

Field collection of samples

A tissue or hair sample was routinely obtained from tagged marmots at initial capture. Tissue samples were collected from either the ear or skin under the foreleg (preferred because the ear bled excessively) with a 2-mm biopsy punch. Alternatively, a few dozen hairs were pulled from the back near the base of the tail.

Marmots that were not trapped were sampled by wedging a stick, wrapped with packaging tape sticky-side out, across the entrance of a burrow (Floyd et al. 2005) when the focal marmot was known to be inside the burrow. This hair trap was placed in such a way that the animal could not leave the burrow without contacting the stick firmly enough that some hair remained on the tape. Field personnel watched the burrows and

removed the hair traps as soon as marmot had left the burrow to avoid collecting the hair of more than one marmot. This allowed me to use any or all hairs collected from a single hair trap. Hairs were removed from the tape with tweezers and stored in paper envelopes. Tweezers were sterilized in the flame of a cigarette lighter between uses. If conditions warranted, envelopes were stored in the field in zip-lock bags with silica to remove any moisture from the samples. When fewer than 15-20 hairs were obtained in a single sample, an attempt was made to obtain a second sample.

Laboratory analyses

Hair samples were stored with silica gel at room temperature prior to DNA extraction. Extractions of non-invasively collected DNA were processed in a separate building from any tissue samples or PCR (polymerase chain reaction) product to reduce the risk of contamination. The DNeasy Blood and Tissue Kits (QIAGEN) were used to extract DNA from the samples. A maximum of 10 follicles were used when possible, with one negative control included in each batch of extractions to test for contamination.

We screened 24 microsatellite primers that had been developed for use in other sciurid rodents (Table G1 and associated footnote). Of these, 13 were polymorphic in Olympic marmots and amplified consistently. We optimized two multi-plex PCRs and two single locus PCRs for nuclear DNA amplification. The multi-plex reactions contained: 2 μL of DNA extract, 1x QIA multi-plex mix (QIAGEN), and 1x primer mix (each primer concentration of 0.2μM). The single locus reactions, for loci GS17 and MA018, contained: 2 μL of DNA extract, 1x Invitrogen buffer, 0.4x forward and reverse primers, 0.4x dNTPs, $MgCl_2$ (3.5x GS17, 2.5x MA018), and Invitrogen Platinum taq.

The final volume of reaction was 10 μL in all cases. PCR was performed on a thermocycler using a touch-down profile: initial denaturation at 95°C for 5 minutes, followed by 20 cycles with 94°C denaturation for 30 seconds, 90 second annealing step then a 60 second extension step. Starting annealing temperatures are listed in Table G2 and stepped down 0.5°C per cycle. This is followed by an additional 25 cycles at 10°C below the starting annealing temperature with an additional final extension cycle of 5 minutes.

Fluorescently labeled DNA fragments were visualized on an automated capillary sequencer with the GS500 ladder (Applied Biosystems) and analyzed with GeneMapper software v3.7 (Applied Biosystems).

Table G1. Loci identified as polymorphic in Olympic marmots. PCR profiles are as described in the text, with starting annealing temperatures as indicated in the table. All loci which used the same profiles were amplified in the same multiples. The reported allelic diversity (A) is based on 56 individuals from 6 colonies in the northwest (Happy Lake, Mt. Appleton, Swimming Bear Lake, and Mt. Carrie) and southeast (La Crosse Basin and O'Neil Pass) of the park. Additional alleles may be present in other populations at these loci.

locus name[1]	source	PCR profile	size-range	A
SS-Bibl18	(Goossens et al. 1998)	60 TD	139-149	4
SS-Bibl25	(Goossens et al. 1998)	58 TD	134-156	6
SS-Bibl31	(Goossens et al. 1998)	58 TD	152-156	2
St-10	(Hanslik & Kruckenhauser 2000)	58 TD	124-132	2
2g2	(Kyle et al. 2004)	60 TD	120-142	7
IGS-6	(May et al. 1997)	58 TD	116-122	4
GS14	(Stevens et al. 1997)	60 TD	142-146	2
GS17	(Stevens et al. 1997)	50 TD	160-168	5
GS22	(Stevens et al. 1997)	60 TD	177-183	3
MS-45	(Hanslik & Kruckenhauser 2000)	58 TD	112-114	2
MS-47	(Hanslik & Kruckenhauser 2000)	60 TD	179-193	7
MA018	(da Silva et al. 2003)	65 TD	302-308	3
MA091	(da Silva et al. 2003)	60 TD	163-179	5

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[1] In addition, the following loci were screened and determined to be monomorphic: MS53, MS56 (Hanslik & Kruckenhauser 2000); MA001, MA066 (da Silva et al. 2003); SS-Bibl4, SS-Bibl36 (Goossens et al. 1998); 3b1, 2g4, 2h6, 2h15, 2h10 (Kyle et al. 2004).

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